Fission-Fusion and Foraging:

Sex Differences in the Behavioral Ecology of Chimpanzees

(*Pan troglodytes schweinfurthii*)

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Abstract of the Dissertation

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In species characterized by fission-fusion, individuals typically experience fewer constraints of cohesive grouping and have greater control over individual foraging decisions. Fission-fusion is often accompanied by clear sex differences in ranging and association patterns thought to reflect a female strategy of avoiding potential feeding competition (spending more time alone or in smaller parties and in smaller differentiated home ranges) and a male strategy of improving mating success through increased sociality and cooperative territory defense (larger parties, larger home range). While this pattern has been observed in a number of fission-fusion species, little is known regarding how this translates into sex differences in actual feeding and foraging behavior. In this thesis I investigate sex differences in the behavioral ecology of chimpanzees (*Pan* *troglodytes schweinfurthii*) by examining whether: 1) males and females differ in foraging effort and diet quality, 2) males and females respond differently to effects of increased party size, and 3) differences in range use relate to foraging. Data collection focused on comparing the foraging behavior of anestrous females and adult males in the Kanyawara community of Kibale National Park, Uganda from May 2004 to July 2005. Results indicate that while overall feeding behavior was similar, foraging strategies diverged significantly during periods of preferred fruit scarcity. Males and females exhibited a similar pattern of caloric and macronutrient intake. However, females responded more to fruit availability by increasing the time they spent feeding and feeding more on fig fruit when preferred fruits were scarce. Despite the fact that females increased their foraging effort, they were not as energetically efficient as males due to the high energetic costs of reproduction and their choice of fallback foods that were high in absolute caloric value but lower in energy return per unit time as compared to the fallback foods favored by males. Females were more likely to experience costs associated with increased party size, but energetic analysis revealed that they were largely able to avoid such costs by remaining in smaller parties in which they could compensate for increased travel effort with increased intake. Both males and females travelled the same daily distance, visiting patches of similar size and number, but females used a smaller range more intensively indicating that their range use reflects foraging effort more so than male range use. These results provide evidence supporting the hypothesis that female chimpanzees, in contrast to males, remain in smaller parties and use smaller core areas in order to avoid resource competition and improve their access to food resources. The fact that males and females exhibited similar overall foraging effort and obtained a

similar quality diet despite such behavioral differences, indicates that studies of sex differences in foraging require detailed data that incorporates nutritional and seasonal adaptations.

“For I am an engine and I’m rolling on,

Through endless revisions to state what I mean,

For sweetness alone who flew out through the window,

And landed back home in a garden of green”

-Neutral Milk Hotel

For Ethel Pokempner

and those who were lost along the way

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Chapter 1

Introduction and summary of chapters

Socioecological theory is largely based on the conflict between reproductive effort in male and female mammals (Trivers 1972, Wrangham 1979a, Sterck et al. 1997). Females typically invest more energy in parental effort through gestation, lactation and infant rearing while males devote more energy to mating effort, which may include maintenance of larger body size in sexually dimorphic species or increased aggression and agonistic displays through territorial and mate defense (Coehlo 1974, Key and Aiello 2000). Female reproductive success thus primarily depends on the ability to acquire high quality resources, while the reproductive success of a male depends mainly on obtaining access to receptive females (Williams 1966, Trivers 1972, Emlen and Oring 1977, Wrangham 1980). In species characterized by high levels of mate competition, sex differences in diet may be a byproduct of sexual dimorphism due to differences in the costs of maintaining large body mass as well as disparate abilities to exploit certain resources (Clutton-Brock 1977, Illius and Gordon 1987, giraffe: Ginnett and Demment 1997; elephant: Stokke 1999). However, in mammals with low to moderate dimorphism, the high metabolic costs of gestation, lactation, and infant rearing encountered by females, increasing as much as 50% in primates, may supersede the additional body size costs faced by males (Portman 1970, Key and Ross 1999). In cases where female requirements are greater than males, it is expected that females will employ more efficient foraging and energy conservation strategies than males (primates: Nakagawa 2000, house mice: Perrigo and Bronson 1985, Richardson's ground squirrels: Michener 1998, big brown bats: Wilkinson and Barclay 1997, seals: Beck et al. 2003). This distinction has a major impact on mammalian social systems, influencing variation in dominance regimes, mating systems, and ranging patterns (Wrangham 1980, Clutton-Brock 1989).

Fission-fusion social systems are a prominent example of the interplay between sex differences in reproductive effort and social organization. Individuals in fission-fusion groups (communities) travel and forage in subgroups of varying size and composition throughout the day, but share a defined community range (Wrangham 1979a, Goodall 1986). These fluid patterns of ranging and association often vary according to sex as is observed in chimpanzees (*Pan troglodytes*). Philopatric males tend to travel in larger groups and cover the entire community range, whereas females spend more time alone or in smaller parties and concentrate their activity in smaller home ranges dispersed within the community range (Wrangham 1979b, Wrangham and Smuts 1980, Hasegawa 1990).This system is thought to reflect the fact that females are particularly vulnerable to resource competition (Pusey et al. 1997, Wrangham 2000, Murray et al 2006). While males may also be subject to increased feeding competition in larger parties (Murray 2006), studies suggest that they are more likely to benefit from group membership in terms of patrol and hunting success (Watts and Mitani 2002), mating tolerance (Duffy et al. 2007) and the opportunity to establish social bonds and rank relations (Goodall 1986, Nishida and Hosaka 1996).

The social and ecological flexibility of fission-fusion has resulted in chimpanzees serving as illustrative case studies for many social and foraging theories (Chapman and Chapman 2000). Firstly, they are not constrained by the pressures of cohesive grouping which may result in a lack of interindividual variation in foraging decisions due to the need for group synchrony. In addition, like many other primates they are frugivorous and must search for patches distributed in a seasonal habitat (Chapman et al. 1995, Chapman and Chapman 2000). The ability of individuals to join and leave a party in such feeding contexts therefore creates a system in which basic foraging models can be tested relatively free of social constraints. In addition, chimpanzees display a moderate level of dimorphism in body mass and this is therefore unlikely to be a major confounding factor in examining feeding behavior in this species. Chimpanzees therefore offer an ideal system in which to test sex differences in foraging behavior. However, such differences have primarily been described in reference to the female bias in extractive foraging, resulting in increased consumption of insects and nuts, as well as a male bias in hunting and meat consumption (McGrew 1979, Boesch 1981 Goodall 1986 Pandolfi 2003, Doran 1997). In both cases, these behaviors are viewed more as social and cultural phenomena than as adaptations to dietary requirements or foraging strategy (Whiten et al. 2001, Pandolfi et al. 2003, but see Gilby et al. 2007).

In this study I investigate sex differences in feeding ecology in chimpanzees. The goal of this research was to evaluate whether there are sex differences in diet and foraging behavior when individuals are released from group constraints. By looking at this question in the absence of confounding factors such as group cohesion and extensive body mass dimorphism, this study seeks to test basic components of the theoretical model of chimpanzee social organization and relate this to other primate social systems.

I begin by comparing general foraging behavior and diet quality among males and females in chapter 2. Specifically, I investigate whether females, driven by high energetic requirements of reproduction, exhibit greater foraging effort and obtain a higher quality diet or alternatively, whether males, as the dominant sex, enjoy a higher quality diet. I relate foraging behavior to efficiency by measuring actual intake, diet selection and response to preferred fruit availability.

In chapter 3, I examine the relative effects of party size on males and females. The flexibility of fission-fusion provides a natural experimental setting in which to test whether females are more likely to avoid costs of within group scramble competition (WGS) by foraging in smaller parties. In contrast, males are expected to tolerate competition imposed by greater gregariousness in exchange for social and mating benefits. I investigate this relation by comparing effects of party size on intake and locomotor expenditure in males and females.

Finally, in chapter 4, I evaluate whether the commonly observed sex differences in chimpanzee ranging relate to corresponding differences in foraging strategy. In addition to travelling in smaller parties, anestrous females are expected to avoid potential competition by dispersing themselves in smaller core areas of varying quality. Male ranging is expected to maximize access to females either through direct mate defense or resource defense, and chimpanzee males are thus observed to cooperatively defend the community range, travelling farther distances and utilizing the extent of the range. To examine how these patterns are related to foraging I look at how daily travel distance relates to patch use in each sex and compare how males and females use their range.

The chapters in this dissertation are presented as independent papers. However, the topics in each are closely related. The concluding chapter offers a synthesis of these results and puts them in the context of sex differences in other primates and mammals.

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Chapter 2

Sex differences in the foraging ecology of chimpanzees (*Pan troglodytes*)

Abstract

Sex differences in feeding and foraging behavior among mammals are ultimately expected to reflect divergent reproductive priorities. Females are primarily constrained by their ability to meet the high energetic costs of reproduction, whereas male mating success is largely limited by access to receptive females. It is therefore generally expected that females will be more likely to maximize their foraging efficiency in order to maintain optimal maternal condition while males will tend to place greater priority on social and mating tactics. Chimpanzees (*Pan troglodytes*), unlike most primates, are characterized by a fission-fusion social system that allows for greater individual flexibility in foraging. However, how this flexibility translates into sex differences in diet quality, foraging effort and foraging efficiency is unknown. This study therefore examines whether males and females differ in nutritional intake and foraging strategy. Over 1,400 hours of data were collected on 5 adult males and 5 anestrous females in the Kanyawara community of Kibale National Park, Uganda from mid 2004-mid 2005. Using full day focal animal sampling, data on 1) dietary intake, 2) activity, and 3) seasonal variation were collected and combined with an extensive nutritional database for the community. Overall, both males and females consumed about 3,000 kcal on a daily basis (females: 3, 068kcal, males: 3, 247kcal) and spent around 30% of time feeding (females: 32.9% of time, males: 32.7% of time). However, when preferred fruit was limited, females, but not males, increased the time they spent feeding and spent more time feeding on fig fruits compared to males. Males did not change their activity budget but spent more time feeding on herbs as compared to females. Despite the fact that females spent more time feeding on fig fruits than males, males had a higher net caloric intake as they relied more on fallback foods which, while lower in absolute nutrient value, had a higher net caloric return due to higher intake rates. These results indicate that studies of sex differences in foraging behavior must be accompanied by data on nutritional and seasonal intake as differences may be concealed by overall similarities , even in species unconstrained by group cohesion.

Introduction

Sex differences in reproductive priorities often serve as the basis for hypotheses explaining variation in foraging strategy and social organization in mammals (Wrangham 1980, van Schaik 1989, Main et al. 1996). Female are expected to maximize energetic and nutritional intake due to the high costs of reproduction whereas males are expected to maximize time spent acquiring mates (Schoener 1971). In a number of taxa, females may cope with these added costs by spending more time feeding (capuchins: Fragaszy 1986, giraffes: Ginnett and Demment 1997), feeding on higher quality items (red deer: Clutton-Brock et al. 1982, squirrel monkeys: Boinski 1989, elephants: Stokke 1999), feeding at higher rates (bighorn sheep: Ruckstuhl et al. 2003, Soay sheep: Pérez-Barberia et al. 2007), or storing energy more efficiently (seals: Beck et al. 2003) than males. Males on the other hand may reduce foraging effort in favor of activities related to resource and/or mate defense, primarily through direct mate competition or territoriality (baboons: Alberts et al. 1996, ground squirrels: Michener 1998, ungulates: Mysterud et al. 2004, bighorn rams: Pelletier et al. 2006). However, while many studies have documented sex differences in foraging behavior, the relative energetic and nutritional consequences of these differences are less clear (but see Knott 1998, Nakagawa 2000). This is in part due to the confounding effects of sexual dimorphism as well as the constraints of activity synchrony in species living in cohesive social groups. In addition, dominance interactions between individuals limit intake and foraging ability and in most gregarious species, males are dominant to females and may have priority of access when foraging. Thus, it is often difficult to isolate factors driving sex differences in foraging. In this paper I examine sex differences by comparing nutrient intake, foraging effort and foraging efficiency in wild chimpanzees (*Pan troglodytes*).

Unlike most primates, chimpanzees are characterized by a fission-fusion system in which community members share a common home range but travel in dispersed parties of varying size and composition (Wrangham 1979, Goodall 1986). Anestrous females tend to travel in small parties centered around core areas, presumably to avoid competition and secure access to higher quality resources (Wrangham and Smuts 1980, Pusey et al. 1997, Murray et al. 2006, Emery Thompson et al. 2007). Males are philopatric and maximize mating success through maintenance of rank and social bonds (Constable et al. 2001, Boesch et al. 2006, Duffy et al. 2007). They are thus typically more gregarious and found in larger parties that cooperatively defend the community territory (Wrangham 1979, Williams et al. 2004). Such a distinction would suggest sex differences in foraging and intake, but to date, only the well documented male bias in hunting (e.g. meat consumption) and female bias in extractive foraging (e.g. termite fishing and nut pounding) have been documented - neither of which is likely to result in a substantial contribution to overall nutritional intake as they constitute a relatively minor portion of the chimpanzee diet (McGrew 1979, Goodall 1986, Mitani et al. 2002, Pandolfi et al. 2003).

Differences in nutritional intake are often predicted as a result of distinct costs of reproduction. Gestation and lactation are particularly demanding, with energy and protein requirements increasing as much as 50% in primates (Portman 1970, Oftedahl 1984, Aiello and Key 2002). A female's energetic status and overall body condition have also been shown to influence timing of conception, infant survival, and infant growth rate (Altmann 1980, Bercovitch 1987, Koenig et al. 1997, Altmann and Alberts 2005). Such reproductive costs may outweigh those encountered by males due to body size in moderately sexually dimorphic species (males <60% larger than females) (Key and Ross 1999). Chimpanzees are characterized by a relatively low level of sexual dimorphism in body mass (males are 30% heavier than females: Smith and Jungers 1997) as well as extended periods of gestation, lactation and infant development (Goodall 1986, Aiello and Key 2002). Moreover, studies have shown that reproductive parameters such as estrogen level and waiting time to conception are closely linked with fruit availability and presumably energy balance in female chimpanzees (Emery Thompson and Wrangham 2008). It is therefore predicted that female chimpanzees will require a more nutritious, high energy diet as compared to males and that this should therefore translate into greater foraging effort.

Individuals may maximize intake by increasing their foraging effort, selecting for higher quality foods and/or feeding at higher rates. In cohesive species, these strategies may be limited by group level decisions and dominance interactions (Janson 1985, Conradt and Roeper 2000, Vogel 2005). In chimpanzees, males are consistently dominant to females as measured by indicators such as pant-grunts and submissive behavior (Goodall 1986). However, greater flexibility in grouping may allow both males and females to avoid extensive competition and consume a high quality diet, dominated by ripe fruit (Goodall 1986, Conklin-Brittain et al. 1998). Like most primates, they respond to reduced food availability and distribution by increasing time spent feeding (Doran 1997), either increasing or decreasing travel time (Doran 1997, Herbinger et al. 2001, Matsumoto-Oda 2002) or broadening the diet to include a variety of lower quality but readily available fallback foods including pith, leaves, and nuts (Isabirye-Basuta 1989, Furuichi et al. 2001). Chimpanzees may also respond to limited resource availability by reducing party size (Chapman et al. 1995, Doran 1997, Mitani et al. 2002). Since males invest more in maintaining rank relations and are thus often found in larger parties, the ability to adapt their foraging strategy may be more limited than females (Murray et al. 2006).

In this study I test the hypothesis that females, driven by high costs of reproduction obtain a higher quality diet through greater foraging effort and efficiency. Here I define efficiency in terms of 1) diet composition, 2) net energy gain per unit foraging time and 3) response to resource availability. Females are predicted to spend more time feeding on higher quality foods, resulting in a higher net energy gain. Females are also expected to increase their feeding effort and feed on higher quality fallback foods in order to maintain a more consistent intake when preferred foods become scarce. In addition, I consider the alternative hypothesis that males, as the dominant sex, obtain a higher quality diet.

Methods

Study Site and Community

Research was conducted from May 2004 to July 2005 in the Kibale National Park located in western Uganda (site described previously by Chapman et al. 1995, Struhsaker 1997). The majority of the 766 km^2, mid-altitude park is characterized by moist, evergreen forest and includes a mix of swamp, grassland, pine plantations, thicket, and secondary forest. Annual rainfall averages 1,662 mm, with two rainy seasons per year (typically March through May and August through November) (Struhsaker 1997).

This study focused on the Kanyawara community which has been the subject of long-term study by Dr. Richard Wrangham and the Kibale Chimpanzee Project (KCP) since 1987 (Wrangham et al. 1992). During the study period, the community consisted of 55 known individuals including 10 adult males and 14 adult females (11 of which were encountered during this study).

Data Collection

Full day focal follows (Altmann 1974) were conducted on adult males and anestrous females (i.e. pregnant or lactating females) (Table 2.1). Five individuals of varying rank and age were sampled from each sex in order to obtain a consistent and unbiased sample of the community throughout the study period. Each female traveled with at least one infant and one juvenile during the study. If a female focal animal came into estrus, she was not followed during the phase of maximal anogenital swelling (typically lasting 10-12 days (Goodall 1986)) in order to avoid confounding socio-sexual influences. Complete nest to nest follows were not always possible (mean follow = 9.2 hours), thus partial day follows consisting of over 5 hours of observation were also included as they closely approximated full day values. Focal follows were distributed evenly by sex and season (Table 2.1).

Behavioral Data

During focal follows, activity was recorded using one minute instantaneous sampling (Altmann 1974). Activity was categorized as feeding, traveling, resting, social, and other. Travel was further classified to reflect different energetic costs (e.g. terrestrial quadrupedal walking, arboreal quadrupedal walking, climbing, and descending). Travel distance on the ground was measured continuously by pacing behind the focal animal. All arboreal travel distance was visually estimated.

When the focal individual was feeding, the species, plant part, and phytophase (e.g. ripe, unripe, young, mature) of the food were recorded. Intake rates were recorded opportunistically and were measured as the number of items (e.g. fruits, leaves) ingested during a continuous 60 second interval. If the food item was large, the percentage of the item consumed during the interval was recorded and converted to an estimated weight. When feeding on pith, intake was estimated and verified by collecting the remnant peel after the focal individual had moved on. I attempted to sample at least ten intake rates per individual per food item. In cases where this was not possible (n=19 out of 240 cases) I assigned an estimated rate based on the average for individuals of the same sex. Intake rates for meat consumption were estimated based on calculations from Boesch (1994).

Nutritional Data

Nutritional data for all major foods eaten by the Kanyawara community were provided by Dr. Nancy-Lou Conklin-Brittain and Dr. Richard Wrangham of Harvard University (see Conklin-Britain et al. 1998, 2006). Measurements included concentrations of crude protein, water soluble carbohydrates (WSC), total nonstructural carbohydrates (TNC), lipids, neutral detergent fiber (NDF), acid detergent fiber (ADF), hemicellulose (HC), and condensed tannins (CT). Additional food items that were underrepresented or absent in the existing database were collected during this study (n= 29 items). Samples were collected as close as possible to the location where an individual was observed feeding and transported back to the research camp. For each sample item (minimum of 10 samples per food item), the whole wet weight was recorded and the item was separated into component parts (e.g. seed, pulp, skin, peel, pith) before being dried in an onsite dryer, reweighed to the nearest gram, and stored for transport. Macronutrient analyses of newly collected items were conducted by the laboratory of Dr. Joerg Ganzhorn in the Department of Ecology and Conservation, Hamburg University. Methods used were comparable to those of Dr. Conklin-Brittain (Ganzhorn and Harthun 2000, Conklin-Brittain et al. 1998).

Energy content was calculated using standard physiological fuel values of 4 kcal/g carbohydrate, 4 kcal/g crude protein, and 9 kcal/g lipid based on human data (National Research Council 1980). Since chimpanzees may be able to extract additional energy from NDF through fermentation, an alternative measure of potential energy including fermentation was calculated using the physiological fuel value of 1.5kcal/g NDF (Milton and Demment 1988, Conklin and Wrangham 1994, Conklin-Brittain et al. 2006). All nutritional values are presented in terms of percentage of organic matter (OM) (Conklin-Brittain et al. 2006). Nutritional information was available for items representing 93% of total feeding time (n=51 food items). The nutritional values for items constituting an additional 5% of feeding time (n= 7 food items) were estimated based on data for similar items, or, in the case of meat, based on the mean value for African bushmeat (Ntiamoa-Baidu 1997) as per Boesch (1994).

Analysis

Intake

Total intake was determined as the total energetic and macronutrient intake, calculated as:

$$\text{Total intake} = \Sigma\,(T_i \times IR_i \times ENC_i)$$

Where T_i is the time spent feeding on food item *i* in minutes, IR_i is the average ingestion rate for food item *i* in grams dry weight per minute, and ENC_i is the caloric or nutritional content of food item *i*. For each focal individual, IR_i was calculated as the product of the average intake rate and the weight of food item *i*. Intake was analyzed using measures of 1) total daily intake based on the data set containing only nest to nest follows (females: n=32 days, male: n=25 days), 2) hourly intake based on the full dataset containing all follows greater than 5 hours (females: n= 691 hrs, males: n=682 hrs) , 3) and intake per unit body mass (kg) to control for sex differences in body mass (using both full day and complete data sets).

Foraging Effort

Foraging is defined in terms of the exploitation of food resources as well as the search for new resources (Janson 1988). Chimpanzees may often travel long distances between major food patches and food oriented travel could therefore not be reliably distinguished from travel in general. I therefore use time spent traveling both within and between food patches as a proxy for search time. There is a possibility that this definition could introduce a bias since chimpanzee males occasionally go on extended patrols of the territory (Mitani and Watts 2005). However, patrols were rare during this study period and did not occur on any of the focal follow days used in this analysis. Time spent foraging was therefore defined as the cumulative time spent feeding and travelling within and between food resources.

Foraging Efficiency

Diet Composition

The diet composition of males and females was measured as the time spent feeding on different food categories (non-fig fruit, fig fruit, pith, herb leaves etc.). Since there is typically high variability in nutrient content and ingestion rates within food categories, I also evaluated time spent feeding on specific food items (Schuelke et al.

2006). Time spent feeding is expressed as the percentage of total observation time in order to control for unequal observation time among individuals. Foods were assessed by comparing absolute nutrient content and nutrient intake rate (defined as nutrients ingested per minute). Nutrient intake rates were calculated for each sex as the product of the mean ingestion rate (grams/min, as calculated above) and the nutrient content (nutrient per gram).

Net Foraging Efficiency

Calculations of net foraging efficiency follow those used by Stacey (1986):

$$\text{Net Foraging Efficiency} = \frac{E_i - E_f}{T_f}$$

where E_i is the total energy intake (calculated as per above), E_f is the total energy expended while foraging, and T_f is the time spent foraging. In this study, foraging is measured as feeding (handling and ingestion of a food item) in addition to travel (both within and between food patches).

Energy expenditure while feeding was calculated as

$$A = (C_i \text{ x BMR x } T_i)$$

where C is the energy constant for feeding (derived from Coehlo 1974 as adjusted in Leonard and Robertson 1997: $C_{feed} = 1.38$), BMR is the basal metabolic rate and T is the time spent feeding in hours. BMR was calculated using the allometric relation described by Kleiber (1961):

$$BMR = 70W^{0.75}$$

where W is an animal's body weight in kilograms. Weights were based on Smith and Jungers (1997) with a mean of 42.7 kg for adult males and 33.7 kg for adult females.

To calculate expenditure during both terrestrial and arboreal quadrupedal walking, I adapted the equation given by Taylor et al. (1982) for primate locomotion:

$$\mathrm{kcal}_{\mathrm{walk}} = (0.0025 \times W^{0.702})\, D + (0.0017 \times W^{0.843})\, T$$

Where D is distance traveled in meters and T is time spent traveling in seconds. It has been noted that the equation developed by Taylor et al. (1982) may overestimate travel costs in chimpanzees since it was based on a primate sample including only juvenile chimpanzees (Pontzer and Wrangham 2004). While this might impact the absolute measurements of expenditure, the relative sex differences should remain unbiased.

I used Hanna's (2006) equation for the cost of transport during climbing since she found that the mass specific cost of climbing remains constant across primates of different body mass:

$$\mathrm{COT}_{\mathrm{climb}} = (106.17)\,(W)^{-0.098}$$

where $\mathrm{COT}_{\mathrm{climb}}$ is measured in Joules $\mathrm{kg}^{-1}\ \mathrm{m}^{-1}$. The relation 1 Joule: 0.00024 kcal was used to convert energy expenditure to kilocalories.

To calculate energy expended while descending a vertical support, I used the equation for potential energy

$$E_{PE} = W\ G\ D$$

where W is mass in kilograms, G is the force of gravity and D is distance traveled in meters. This was converted to metabolic energy by dividing by an efficiency of 95% and converting to kilocalories (Warren and Crompton 1998).

The additional costs of pregnancy, lactation and infant transport were factored into expenditure calculations for reproductive females. Expenditure for pregnant and lactating individuals was multiplied by a factor of 1.25 and 1.5 respectively to compensate for increased costs of reproduction (Portman 1970, Oftedahl 1984, Key and Ross 1999, Aiello and Key 2002). Infants were divided into three age categories (0-6mo, 7mo-2yr, 3-5yr) and weights were assigned based on previously estimated birth weights and growth trajectories (Zihlmann 1997, Pusey et al. 2005). The proportion of time spent carrying an infant of a given class was calculated based on focal scan data and the locomotor expenditure was adjusted for the added infant weight by multiplying by a constant (1.05, 1.15, and 1.30 respectively).

Seasonal Response

In order to investigate variation in intake and foraging according to resource availability, I defined two distinct seasons based on the presence or absence of preferred non-fig fruit species in the diet. Long-term research at Kibale indicates that the chimpanzees exhibit a clear preference for certain non-fig, or succulent drupe, fruit species including *Mimusops bagshawei, Pseudospondias microcarpa,* and *Uvariopsis congensis* (Wrangham et al. 1996, Emery Thompson 2005). In a previous study of the Kanyawara community, Sherry (2003) found that time spent feeding on preferred fruits was correlated with fruit availability. These species tend to fruit synchronously at the intraspecific level but asynchronously at the species level. This results in clear and isolated periods of preferred fruit availability during which these foods dominate the chimpanzee diet (Chapman et al. 1999). Figs, in contrast, are available year round but are unpredictable and scattered throughout the range (Chapman et al. 2005). Therefore, using similar methods to previous studies at this site (Emery Thompson 2005, Gilby and Wrangham 2007), the season was defined as the “non-fig fruit season” (NFF) if over 40% of the diet consisted of preferred fruit for three consecutive days. All other days were attributed to the “fig fruit season” (FF). During the study period, the non-fig fruit season corresponded to two major periods including September to December and March to May.

Statistical Analysis

General linear models (GLM ANOVA) were used to examine sex differences in intake and foraging parameters. Individuals were considered as independent samples (n= 10). Results based on the analysis of intake from the full day follow data subset are presented unless analysis of the complete dataset yielded different results. Seasonal variation within each sex was examined using a repeated measures design. In order to investigate variation in quality among different food categories I used a GLM ANOVA with a post-hoc Tukey test for unequal sample size. All proportional data were arcsine transformed to conform to the assumptions of normality. All tests were conducted using SPSS v. 13.0.

Results

Intake

Overall, males and females exhibited similar intake patterns. Absolute daily intake did not differ in terms of total dry weight or caloric intake (Table 2.2). There was also no significant difference in total daily macronutrient intake (Figure 2.1). However, when calculated relative to body weight, females had a significantly higher intake of nonstructural carbohydrates (females: 11.4 ± 1.1 g/kg , males: 8.9 ± 2.1 g/kg, $F_{(1, 8)}$ = 5.410, p =0.04) and showed a tendency towards higher caloric intake (females: 91.1± 8.8 kcal/kg , males: 76.0 ± 15.0 kcal/kg;, $F_{(1, 8)}$ = 3.742, p =0.08). A comparison of hourly intake (both absolute and standardized by body weight), using the complete data set, yielded similar results with the exception that males exhibited a higher absolute intake of calories (females: 202.1 ± 20.2 kcal /hr, males: 233.6 ± 22.2 kcal /hr, $F_{(1, 8)}$ = 5.483, p = 0.04) and protein (females: 12.2 ± 1.8 g/hr, males: 16.1 ± 2.6 g/hr, $F_{(1, 8)}$ = 7.711, p = 0.02).

Foraging Effort

There was no sex difference in overall foraging effort. Males and females spent 32.7% and 32.9 % of their time feeding ($F_{(1, 8)}$ = 0.059, p =0.81) and 10.2% and 10.1% of their time traveling ($F_{(1, 8)}$ = 0.022, p =0.89) respectively. As there was no sex difference in daily active period (defined as the time between leaving the morning nest to building the night nest), these proportions were directly comparable (females: 11.3 ± 0.6 hrs, males: 11.7 ± 0.3 hrs, $F_{(1, 8)}$ = 1.08, p=0.34).

Foraging Efficiency

Diet Composition

Overall males and females spent a similar amount of time feeding on both non-fig ($F_{(1, 8)}$ =0.004, p=0.95) and fig fruit ($F_{(1, 8)}$ = 1.993, p =0.20) (Table 3). However, females spent more time feeding on mature tree leaves ($F_{(1, 8)}$ = 8.880, p =0.02) while males spent more time feeding on herb leaves ($F_{(1, 8)} = 10.601$, $p = 0.01$) and pith ($F_{(1, 8)} = 4.088$, $p = 0.08$) (Table 2.3). Although only males were observed to consume meat (0.51 ± 0.61% of total observation time), the rare occurrence during the study period did not allow for a statistical comparison. An evaluation of food groups indicated that new leaves and herbs had higher concentrations of protein than pith, and all fruits ($F_{(7, 49)} = 6.797$, $p < 0.001$). Shrub fruits contained higher levels of water soluble carbohydrates than fig and non-fig fruit, mature leaves, pith and herbs ($F_{(7, 49)} = 6.307$, $p < 0.001$) and more total nonstructural carbohydrates than herbs, new leaves and pith ($F_{(7, 49)} = 3.554$, $p < 0.01$).

Net Foraging Efficiency

Males exhibited a higher overall net foraging efficiency than females regardless of whether caloric intake was measured using the lower or upper limit of fermentation (no fermentation: females: 5.6 ± 0.8 kcal /min, males: 7.1± 0.7 kcal /min, $F_{(1, 8)} = 9.242$, $p = 0.02$; fermentation: females: 8.2 ± 1.0 kcal /min, males: 9.9 ± 1.0 kcal/min, $F_{(1, 8)} = 7.850$, $p = 0.02$).

Seasonality

Both males and females suffered a decrease in diet quality when preferred fruit became scarce. Specifically total dry weight and caloric intake was significantly lower in the FF season (Table 2.4).This was reflected in a decrease in carbohydrate and hemicellulose consumption (Figure 2.2). Although absolute intake of NDF and ADF did not vary by season, the relative proportion of fiber in the diet increased for both males and females when preferred fruit was limited (females ADF: $F_{(1, 4)} = 9.830$, $p = 0.04$, NDF:

$F_{(1, 4)}$ = 6.760, p=0.06; males ADF: $F_{(1, 4)}$ = 15.702, p=0.02, NDF: $F_{(1, 4)}$ = 12.743, p=0.02) (Figure 2.2). These results did not differ depending on dataset used or whether standardized by body weight.

When preferred fruit was scarce, females significantly increased the time they spent feeding (NFF: 29.9 ± 1.6% of time, FF: 35.7 ± 1.9% of time, $F_{(1, 4)}$ = 81.73, p = < 0.01) and showed a slight but non significant increase in travel time (NFF: 9.2 ± 1.9% of time, FF: 10.9 ± 2.1% of time, $F_{(1, 4)}$ = 0.955, p = 0.38) (Figure 2.3). Males did not significantly alter their activity in response to availability. Neither sex changed their total daily active period across season (females: NFF 11.1 ± 0.7 hours, FF 10.8 ± 0.4 hours, $F_{(1, 4)}$ = 3.231, p=0.15; males: NFF: 11.1 ± 0.6 hours, FF 10.6 ± 0.9 hours, $F_{(1, 4)}$ = 5.103, p=0.09), meaning that there had to be a trade off in female activity budget due to the increase in feeding time. Further investigation revealed that there was a significant negative relation between feeding time and resting time in females (Pearson correlation coefficient: -0.860, p<0.01) . Although males did not show a seasonal change in feeding time, any increase in feeding came at the cost of time spent in social activities (Pearson correlation coefficient: -0.264, p=0.02).

Males and females also differed in their use of fallback foods. Based on the definition of season used in this study, all individuals spent more time feeding on figs when preferred fruit was scarce. However, females increased fig feeding to a greater degree (sex by season interaction: $F_{(1,8)}$ = 5.94, p =0.04) (Figure 2.4). Females also increased the time they spent feeding on pith (NFF: 1.5 ± 1.4 % of time, FF: 4.2 ± 1.39% of time, $F_{(1,4)}$ = 21.570, p =0.01) while males increased the time they spent feeding on herb leaves (NFF= 1.4 ± 1.1% of time, FF = 4.8 ± 1.9% of time, $F_{(1,4)}$ = 9.49, p = 0.03).

Analysis by food item indicated a significant sex difference in time spent feeding on the fig fruit *Ficus exasperata* ($F_{(1,8)} = 8.796$, $p = 0.02$) and the herb leaf *Lepistemon owariense* ($F_{(1,8)} = 7.268$, $p = 0.03$) (Table 2.5). Qualitative comparison of the two plant foods reveals that *F. exasperata* is higher in carbohydrates and lower in fiber on a per gram basis when compared to *L. owariense*. However, *L. owariense* was eaten at a higher nutrient intake rate in terms of both protein and calories per minute (Table 2.5). Females also fed more on the high calorie shrub fruit *Phytolacca dodecandra* than males when preferred fruit was scarce ($F_{(1,8)} = 5.553$, $p=0.05$) (Table 2.5).

Both males and females exhibited a lower net foraging efficiency in the FF season relative to the NFF season (females: $F_{(1,4)} = 32.671$, $p<0.01$, males: $F_{(1,4)} = 42.451$, $p<0.01$). Males had a higher net efficiency as compared to females only during the fig season but not the non-fig season (Table 2.6).

Discussion

Contrary to the predictions, male and female chimpanzees showed little difference in overall intake and foraging effort. Although females consumed more carbohydrates when body weight was controlled for, males had a similar, if not higher, absolute energetic and nutritional intake despite devoting the same amount of time to foraging. Males were thus found to forage more efficiently overall as compared to females. These results might be expected based on body size dimorphism alone (27% higher requirements in males), but when the added costs of reproduction in chimpanzees are factored in (anywhere from 35-65% higher than baseline levels in females) female energetic requirements should exceed those of males (Key and Ross 1999). However, these costs to females may be overestimates as they are likely to be more variable across species and the reproductive cycle (Aiello and Key 2002). While female chimpanzees are expected to have high long-term requirements of lactation due to long interbirth intervals, the daily costs may be reduced (Dufour and Sauther 2002). It is therefore possible that short-term energetic costs for male and female chimpanzees are in fact similar (Key and Ross 1999), resulting in the similar patterns of intake observed in this study. Recent research on chimpanzee hormonal function suggests that energy intake may be more important at certain phases such as conception when females tend to peak in energy intake (Emery Thompson 2005). It may therefore be possible that sex differences in energy intake are limited to these phases.

Alternatively, a female's ability to maximize intake may also be constrained by male dominance. While male aggression through sexual coercion has been well documented in chimpanzees (Wrangham 2002, Muller et al. 2007), the effects of male dominance in feeding contexts is less clear. In a study evaluating the relation between chimpanzee rank and access to higher quality regions within a feeding tree, no difference in feeding location was found based on sex (Kahlenberg 2006). In the current study, 40% of male aggression directed toward the focal females occurred while feeding (Pokempner, unpublished data). At Gombe, 12% of male–female aggression (including females of all sexual states) was observed in the context of feeding, with the majority of this aggression occurring during meat eating (Goodall 1986). If male aggression does directly limit female feeding, this should result in reduced intake, particularly in contestable fruit patches (van Schaik and van Noordwijk 1988). However, although this study did not test the effects of intersexual competition, the results indicate that females in fact fed on more fruit than males when resources were scarce. It is perhaps more likely that male dominance has an indirect effect on female feeding as mothers may choose to avoid males (Otali and Gilchrist 2006) or leave a patch upon the approach of males (pers. obs.)

While overall intake was similar between the sexes, the strategies used to obtain these nutrients were not. Males and females primarily differed in their response to the seasonal availability of preferred fruits. Females responded to reduced availability by increasing the time they spent feeding, and specifically feeding more on fig fruits. Males did not change their activity budget, but relied more on herbs, in addition to figs, when preferred fruit was scarce. In a study of female foraging in Gombe, Murray et al. (2006) also found that chimpanzee females increased their foraging effort in response to limited resources. They concluded that these females experienced less seasonal variation in diet quality, as defined by the time spent feeding on presumed low quality items such as pith and leaves. Rather, it was suggested that males would be more vulnerable to fluctuations in resources due to constraints of male sociality (Murray et al. 2006). While the results of the current study support these predictions based on activity and diet alone, the nutritional data indicate that both males and females suffered a similar decrease in diet quality despite seemingly different strategies.

Males were found to have a higher feeding efficiency in comparison to females when preferred fruit was scarce. Given the similarity in intake and activity, this difference in efficiency may in part be explained by the fact that energetic expenditure in females was compounded by added costs of reproduction that were factored into the calculations. In addition, this difference may be due to the fact that males fed more on fallback foods that were lower in nutritional value but could be processed more quickly.

During the fig season *L. owariense* contributed over 15% to male caloric intake and ranked as the second top food for males. Similarly, in a study of capuchins (*Cebus capucinus*), Rose (1994) found that males spent less time feeding than females but may have had a greater intake since they devoted more time to feeding on items with less handling time. A number of studies of primate foraging have shown that the ingestion rate of a food may be as important, if not more so, than the nutritional content in determining food choice and total intake (Hladik 1977, Barton and Whiten 1994, Nakagawa 1997, Schuelke et al. 2006). For males, selecting fallback foods based on intake rates may fit more with a time minimizing strategy that would allow them to conserve their social time across seasons since feeding time and social activity were found to be inversely related. Goodall (1986) suggested that competition for estrous females and participation in patrols led to decreased feeding in males. Males may therefore compensate through food choice based on intake rates.

However, these results must be viewed with caution as they do not factor in the relative effects of digestion. Calculations used to determine energy intake and net foraging efficiency rely on measures of digestibility, but do not account for individual differences in gut passage rate (Conklin-Brittain et al. 2006). Ideally, digestion should be considered as a component of handling time and may vary by food (Courtney and Sallabanks 1992, Bozinovic and Torres-Contreras 1998). Since more fibrous foods will take longer to process in the gut, there may be a delay in the relative availability of this energy (Milton and Demment 1988). Additionally, there is no evidence of a significant sex difference in gut size or retention times that would suggest that male chimpanzees are more efficient at extracting nutrients from fiber due to larger body size as is the case in some more dimorphic species (Lambert 2002). The calculations used here may therefore overestimate the energy content of these foods.

Measuring quality, particularly from the perspective of the foraging animal is thus more complex (Janson et al. 1986). Research on primates suggest that individuals use a variety of sensory cues to determine ripeness and nutritional content of fruits and leaves – specifically in terms of sugar content (Riba Hernandez et al. 2005, Dominy et al. 2006). Chimpanzees are known to select for fruits high in sugars (Reynolds et al. 1998, Matsumota-Oda and Hayashi 1999) and leaves high in protein (Takemoto 2003). In this study, females were found to feed more on the fruits *F. exasperata* and *P. dodecandra* , both of which had high levels of sugar on an absolute basis. In addition, fig fruits from Kibale are high in calcium compared to other foods (O'Brien et al. 1998), and this may be particularly important to mothers during lactation (Galloway 1997). This would suggest that females may be following an energy maximizing strategy by spending more time feeding on foods with higher sugar content and more readily available energy as perceived by physical traits such as ripeness.

The overall similarity between the sexes observed in this study is unexpected given the that individuals in a fission-fusion society can forage independently, thus allowing greater variation among males and females. However, despite flexible grouping, chimpanzees may still be subject to social constraints that limit foraging options. The "social factors" hypothesis maintains that male chimpanzees will favor resources that allow for foraging in larger social groups (Boesch and Boesch 1984). This hypothesis is typically applied to sex differences in tool use and hunting, in chimpanzees (Pandolfi et al. 2003). This same logic may extend to feeding on pith and herbs (terrestrial herbaceous pith and leaves or TPL) as these resources usually occur in superabundant, non contestable patches which allow for larger feeding parties (Wrangham 1986, Wrangham et al. 1996). It would therefore follow that males may be more likely to feed on TPL, particularly when fruit patches are small and scattered. While Malenky and Wrangham (1994) found that there was no difference in party size in fruit or TPL patches, they did not differentiate between males and females. The fact that males in this study spent more time feeding on herbs, particularly when preferred fruit was scarce, suggests that this may be a social tactic that allows males to maintain high levels of gregariousness throughout the year. Although party size was not included in this analysis, it is likely to be an important factor in distinguishing male and female foraging constraints (Wrangham 1986).

In addition, the difference detected in diet composition may reflect a sex difference in range use. Female chimpanzees are commonly observed to be more arboreal than males (Wrangham and Smuts 1980, Hunt 1989, Doran 1993, Takemoto 2004). This difference may reflect the greater reliance of males on terrestrial vegetation since an increase in terrestriality was associated with TPL feeding at Bossou (Takemoto 2004). Although there are a number of factors that may influence differences in arboreality, including ecological factors and degree of habituation (Wrangham 1977, Takemoto 2004), it is also possible that this may be due to a sex difference in predation risk as females, travelling alone and in smaller parties with their offspring, may be more reluctant to feed in the often open and exposed TPL patches.

In summary, while females displayed more foraging effort in response to fluctuations in resource availability, males were actually more energetically efficient.

Overall, these differences were concealed by generally similar patterns of feeding behavior and intake. Across primates, sex differences in feeding ecology are influenced by a number of factors including social organization, body mass dimorphism, and diet choice with no clear pattern emerging (Clutton-Brock 1977, Pandolfi 2005, Kamilar and Pokempner 2008). In many ungulates and solitary species, sexual segregation is more common, often reflecting body size dimorphism and a sex differences in activity asynchrony (Ruckstuhl and Kokko 2002, Du Toit 2005). Since chimpanzees conform to the gregarious social pattern common to most primates, but employ a more flexible grouping system that is similar to that observed in many sexually segregated species, they serve as an important study system in the spectrum of the evolution of sex differences (Watts 2005). Despite the relatively constraints free social organization of fission-fusion, male and female chimpanzees were found to exhibit similar overall foraging behavior and consumed a similar quality diet. Females adjusted their behavior more in times of preferred fruit scarcity by devoting more time to feeding and specifically feeding more on fig fruit. However this did not translate to an increase in intake due to the fact that these fruits were high in absolute nutritional content, but lower in caloric return per minute in comparison to the fallback foods preferred by males. While there may be a number of social and physiological reasons (discussed above) for this sex difference in consumption of fallback food, this study illustrates the importance of quantifying diet in terms of both nutritional content and seasonal adaptations. In many primate studies, sex differences in foraging are reported as absent or not noted at all. The results of this study indicate that a lack of difference in overall parameters such as feeding time and diet composition may give a false impression of similarity and may conceal more subtle differences in foraging strategy.

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Table 2.1 Summary of focal sample data.

	Focal ID	Rank[a]	Age (years)[b]	Number of dependent offspring[c]	Number of days sampled	Number of hours sampled	Number of days sampled by season[d]
Females	AL	6	26	1.5	14	135	9/5
	BL	1	47	2	15	135	7/8
	NL	7	25	2	13	123	6/7
	OU	2	28	3.5	17	161	9/8
	TG	5	27	2	15	137	9/6
Males	AJ	5	30		14	126	7/7
	KK	2	19		15	145	7/8
	LK	6	22		15	123	7/8
	MS	1	29		14	134	7/7
	YB	10	31		17	154	9/8
				Total	**149**	**1,373**	**77/72**

[a] Female rank for the period 1997-2003 taken from Kahlenberg 2006, Male rank for 2004-2005 courtesy of Kahlenberg, Muller and Wrangham pers. comm. Rank determined based on direction of pant grunts and outcome of dyadic aggressive interactions. In each case, 1 indicates alpha rank, followed by subsequent rank order out of all adult individuals for each sex.

[b] Age estimates based on KCP long-term records

[c] Number of dependent offspring expressed as average number of infants and juveniles (age 0-7yrs) traveling with the mother during the study period

[d] The number on the left refers to days sampled during the fig season; the number on the right refers to the non-fig season

Data include all focal observations greater than 500 min per day

Table 2.2 Sex specific overall daily dry weight and caloric intake. Values are based on data subset consisting only of full day, nest to nest follows.

	Mean Daily Intake		
	Females	Males	
Total dry weight (g)	1,044.6 ± 89.7	1,110.7 ± 237.0	$F_{(1,4)}$=0.340, p=0.58
Caloric intake: no fermentation (kcal)	2,323.0 ± 245.4	2,445.1 ± 482.4	$F_{(1,4)}$=0.254, p=0.63
Caloric intake: fermentation (kcal)	3,068.6 ± 296.0	3,247.0 ± 639.1	$F_{(1,4)}$=0.321, p =0.59

Table 2.3 Sex differences in diet by food group

Time spent feeding on different food groups is calculated as the mean proportion of total observation time for the five individuals in each sex (n= 691 hours for females and 682 hours for males). Nutritional content is expressed as percentage of organic matter. WSC= water soluble carbohydrates, TNC = total nonstructural carbohydrates, NDF= neutral detergent fiber, ADF = acid detergent fiber, HC = hemicellulose, CT = condensed tannins. For each food category, n indicates the number of food items analysed.

	% Time Spent Feeding			**Nutritional Content**									
	Females	**Males**		**kcal/100 g (no fermentation)**	**kcal hi/100 g (fermentation)**	**Lipid**	**Protein**	**WSC**	**TNC**	**NDF**	**ADF**	**HC**	**CT**
Non Fig Fruit	**12.2**	**12.2**		**283.8**	**345.2**	**8.1**	**12.6**	**20.6**	**40.2**	**40.9**	**25.5**	**13.2**	**3.9**
n=13	±2.3	±1.4		±136.9	±124.8	±17.3	±10.6	±10.4	±17.7	±11.1	±8 .2	±8.3	±6.0
Fig Fruit	**9.6**	**7.3**		**225.6**	**299.4**	**4.5**	**9.6**	**12.6**	**36.7**	**49.2**	**41.5**	**7.6**	**4.5**
n=6	±3.1	±1.8		±50.3	±30.9	±2.2	±5.6	±3.5	±15.6	±13.3	±14.3	±2. 0	±4.4
Herb Leaf	**1.0**	**3.2**	**p=0.01**	**223.0**	**294.4**	**2.3**	**26.1**	**5.7**	**24.6**	**47.6**	**28.9**	**18.7**	**3.2**
n=5	±0.9	±1.2		±58.3	±33.0	±1.6	±3.2	±1.1	±17.0	±17.0	±8.1	±14. 8	±7.0
Pith	**3.0**	**4.6**	**p<0.10**	**155.8**	**248.7**	**0.7**	**11.5**	**14.8**	**25.8**	**61.9**	**40.0**	**21.9**	**0.3**
n=7	±1.4	±1.4		±48.0	±30.5	±0.7	±9.4	±4.7	±8.7	±11.7	±7.4	±6.8	± 0.6
New Tree Leaf	**4.2**	**3.8**		**223.2**	**292.3**	**1.5**	**28.0**	**5.6**	**24.4**	**46.8**	**31.0**	**14.4**	**7.2**
n=11	±1.4	±1.9		±41.1	±25.5	±1.1	±7.6	±2.8	±8.8	±10.6	±10.1	±3. 5	±8.9
Mature Tree Leaf	**1.3**	**0.3**	**p=0.02**	**218.6**	**288.4**	**1.0**	**24.4**	**7.3**	**27.8**	**46.5**	**19.1**	**2.2**	**0.4**
n=2	±0.8	±0.2		±15.4	±7.1	±1.3	±1.3	±8.3	±5.6	±5.5	±27.0	±3.1	±0 .0
Shrub Fruit	**0.8**	**0.8**		**303.1**	**348.0**	**4.6**	**11.8**	**35.5**	**53.8**	**29.9**	**22.6**	**7.0**	**3.2**
n=5	±0.6	±0.6		±79.6	±53.6	±3.7	±6.5	±23.7	±17.6	±18.0	±12.9	±5 .6	±6.0
Other	**0.7**	**0.7**		**168.8**	**257.8**	**1.2**	**10.4**	**15.3**	**29.1**	**59.3**	**45.2**	**14.1**	**0.0**
n=3	±0.4	±0.6		±141.8	±87.2	±0.8	±11.7	±20.0	±25.5	±36.4	±32.5	±4.0	±0.0

Table 2.4 Seasonal variation in daily intake

NFF= Non fig fruit season**,** FF = Fig fruit season. Statistics for seasonal differences within the sexes are listed across rows. Statistics for sex differences within seasons are listed in columns. Caloric intake measured as total kcal consumed per full day. For females, n= 34 days in the NFF season, 40 days in the FF season. For males, n= 38 days in the NFF season, 37 days in the FF season.

	Total Dry Weight (g)			**Caloric Intake: No Fermentation**			**Caloric Intake: Fermentation**		
	NFF	**FF**	**Between seasons**	**NFF**	**FF**	**Between seasons**	**NFF**	**FF**	**Between seasons**
Females	1,159 ± 61	927 ± 175	$F_{(1,8)}=8.70$, $p=0.04$	2,747 ± 300	1,842 ± 364	$F_{(1,8)}=25.42$, $p<0.01$	3,500 ± 270	2,596 ± 487	$F_{(1,8)}=18.47$, $p=0.01$
Males	1,296 ± 312	930 ± 196	$F_{(1,8)}=22.24$, $p<0.01$	2,932 ± 676	1,952 ± 389	$F_{(1,8)}=17.59$, $p=0.01$	3,827 ± 898	2,670 ± 510	$F_{(1,8)}=17.11$, $p=0.01$
Within season	$F_{(1,4)}=0.93$, $p=0.36$	$F_{(1,4)}=0.00$, $p=0.98$		$F_{(1,4)}=0.31$, $p=0.60$	$F_{(1,4)}=0.22$, $p=0.66$		$F_{(1,4)}=0.61$, $p=0.46$	$F_{(1,4)}=0.55$, $p=0.82$	

Table 2.5 Sex differences in diet during the FF season

Table includes all foods contributing to >1% of total diet during the FF season. Time spent feeding on different foods is calculated as the mean of the proportion of total observation time for the five individuals of each sex (n= 184 hours for females and 140 hours for males). Nutritional intake is calculated as the product of the ingestion rate and nutritional content. A statistical comparison of intake for *P. dodecandra* was not possible due to limited data for males.
* indicates significance at the level of p<0.05.

		% Time Feeding		Intake in kcal/min		Intake in protein/min		Nutritional Intake									
Species	Part	Female	Male	Female	Male	Female	Male	kCal/100g (no fermentation)	kCal/100g (fermentation)	Lipid	CP	WSC	TNC	NDF	ADF	HC	CT
Acanthus pubescens	pith	0.6 ± 0.4	1.2 ± 0.8	7.5 ± 0.4	12.5 ± 2.8 *	0.7 ± 0.0	1.1 ± 0.3 *	238	299	0.3	27.2	15.3	31.7	40.8	28.4	12.4	0.2
Aframomum mildbraedii	pith	0.9 ± 0.9	1.1 ± 0.1	20.4 ± 6.6	23.3 ± 4.6	0.7 ± 0.2	0.7 ± 0.2	122	227	0.5	7.2	7.6	22.0	70.2	46.3	23.9	0.2
Celtis africana	young leaves (buds)	1.2 ± 1.1	2.4 ± 2.3	2.6 ± 0.7	2.7 ± 0.0	0.3 ± 0.9	0.4 ± 0.0	246	304	0.0	39.7	4.1	21.9	38.4	25.9	12.6	4.6
Celtis africana	young leaves	1.1 ± 0.9	0.8 ± 1.1	11.9 ± 2.4	16.0 ± 2.2 *	1.5 ± 0.3	2.0 ± 0.3 *	275	323	0.5	40.6	3.6	27.2	31.7	16.9	14.7	0.1
Cordia abyssinica	non-fig fruit	1.5 ± 0.7	2.2 ± 1.1	13.1 ± 1.9	16.0 ± 0.9 *	0.4 ± 0.1	0.5 ± 0.0 *	218	290	1.9	8.0	24.4	42.0	47.7	30.4	1.7	1.5
Ficus sansibarica (brachylepsis)	fig fruit	2.3 ± 0.9	1.8 ± 1.2	4.0 ± 1.1	8.4 ± 2.1 *	0.1 ± 0.0	0.3 ± 0.1 *	272	327	3.7	10.3	13.0	49.3	36.7	31.5	7.3	1.7
Ficus sur (capensis)	fig fruit	1.6 ± 2.0	1.1 ± 1.5	13.8 ± 3.8	19.1 ± 4.0	0.6 ± 0.1	0.9 ± 0.2	156	264	8.8	13.0	14.5	6.1	72.0	66.6	5.5	13.0
Ficus dawei	fig fruit	1.3 ± 1.2	0.5 ± 0.8	13.8 ± 2.5	15.3 ± 3.8	0.4 ± 0.1	0.5 ± 0.1	208	288	4.4	8.5	6.7	33.6	53.5	45.1	10.3	3.1
Ficus exasperata	fig fruit	3.4 ± 1.0	1.3 ± 1.4 *	8.5 ± 1.8	8.9 ± 0.9	0.6 ± 0.1	0.6 ± 0.1	277	334	6.1	21.8	12.8	33.5	38.6	24.1	9.6	0.9
Ficus exasperata	mature leaves	1.1 ± 1.3	0.3 ± 0.5	16.7 ± 9.6	19.1 ± 0.5	1.5 ± 0.8	1.7 ± 0.0	230	293	0.0	25.6	1.8	31.7	42.6	38.2	4.4	0.4
Ficus natelensis	fig fruit	6.8 ± 4.6	5.4 ± 1.7	9.0 ± 2.5	10.3 ± 1.3	0.2 ± 0.1	0.3 ± 0.0	152	249	1.9	6.5	8.3	27.3	64.3	55.0	9.2	3.1
Lepistemon owariense	herb leaves	0.9 ± 1.4	2.9 ± 1.2 *	18.5 ± 5.5	23.4 ± 2.6	1.8 ± 0.5	2.3 ± 0.3	216	290	2.7	28.8	4.7	19.1	49.5	35.1	14.4	0.0
Linociera johnsonii	non-fig fruit	0.3 ± 0.6	1.5 ± 1.7	17.5 ± 4.2	14.3 ± 2.5	0.6 ± 0.1	0.5 ± 0.1	230	301	3.7	10.3	19.5	39.1	47.0	37.4	9.6	0.7
Marantochloa leucantha	pith	1.3 ± 1.5	1.1 ± 0.9	4.1 ± 1.4	4.8 ± 1.0	0.2 ± 0.1	0.2 ± 0.0	143	240	0.4	9.3	18.1	25.6	64.7	40.8	23.9	0.0
Pennisetum purpureum	pith	1.0 ± 1.1	0.6 ± 0.4	3.2 ± 0.5	3.2 ± 0.3	0.1 ± 0.0	0.1 ± 0.0	116	223	0.3	4.1	18.5	24.2	71.4	46.3	25.1	0.0
Phytolacca dodecandra	shrub fruit	0.8 ± 0.7	0.1 ± 0.1 *	27.6 ± 0.6	13.33 ± 0.0	1.7 ± 0.0	0.8 ± 0.0	347	383	8.8	23.9	34.7	42.8	24.4	18.3	6.1	0.1

Table 2.6 Seasonal variation in foraging efficiency
NFF= Non fig fruit season**,** FF = Fig fruit season. Statistics for seasonal differences within the sexes are listed across rows. Statistics for sex differences within seasons are listed in columns.

	Foraging Efficiency: No Fermentation			**Foraging Efficiency: Fermentation**		
	NFF	**FF**	**Between seasons**	**NFF**	**FF**	**Between seasons**
Females	8.0 ± 1.5	3.8 ± 0.7	F=26.781, p<0.01	10.8 ± 1.7	6.1 ± 0.7	F=32.671, p<0.01
Males	8.6 ± 1.0	5.5 ± 0.8	F=40.683, p<0.01	11.6 ± 1.3	8.2 ± 1.0	F=42.451, p<0.01
Within season	F=0.604, p=0.46	F=12.358, p<0.01		F=0.682, p=0.43	F=14.792, p<0.01	

Figure 2.1 Sex specific daily intake of macronutrients.

Macronutrient contribution expressed in terms of grams. Numbers above bars indicate the percentage of total intake.WSC= water soluble carbohydrates, TNC = total nonstructural carbohydrates, NDF= neutral detergent fiber, ADF = acid detergent fiber, HC = hemicellulose, CT = condensed tannins. For each macronutrient considered, there was no significant difference between males and females (p>0.05).

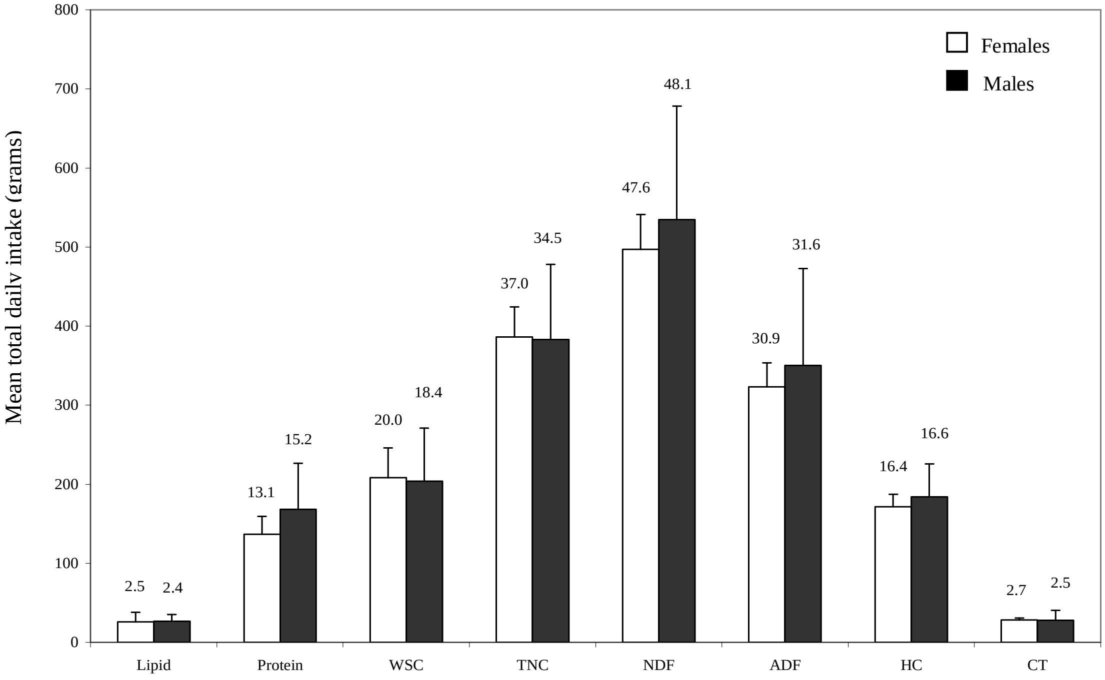


Figure 2.2 Seasonal variation in daily macronutrient consumption
For each sex, bars on the light bars on the left represent the NFF season and the dark bars on the right represent the FF season. Numbers above bars represent proportion of total intake
* indicates significance at p=0.05, ** indicates significance at p =0.01

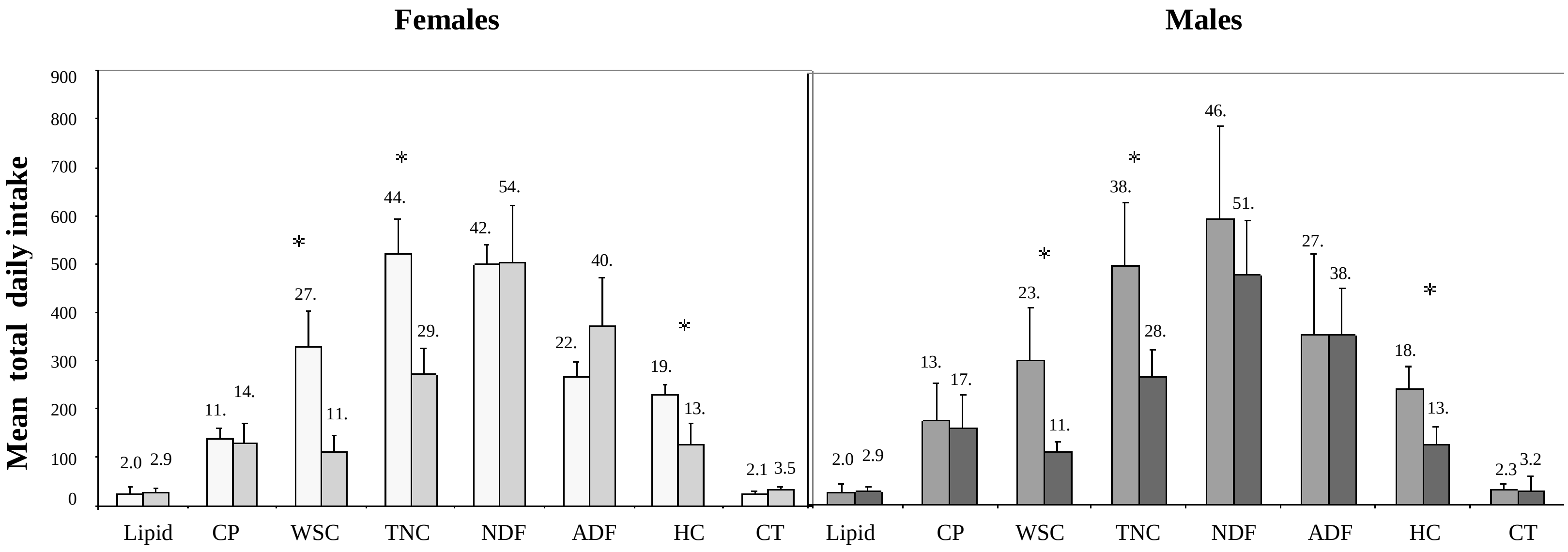


Figure 2.3 Seasonal variation in activity budget

For each sex, bars on the light bars on the left represent the NFF season and the dark bars on the right represent the FF season.

* indicates significant difference at p <0.05

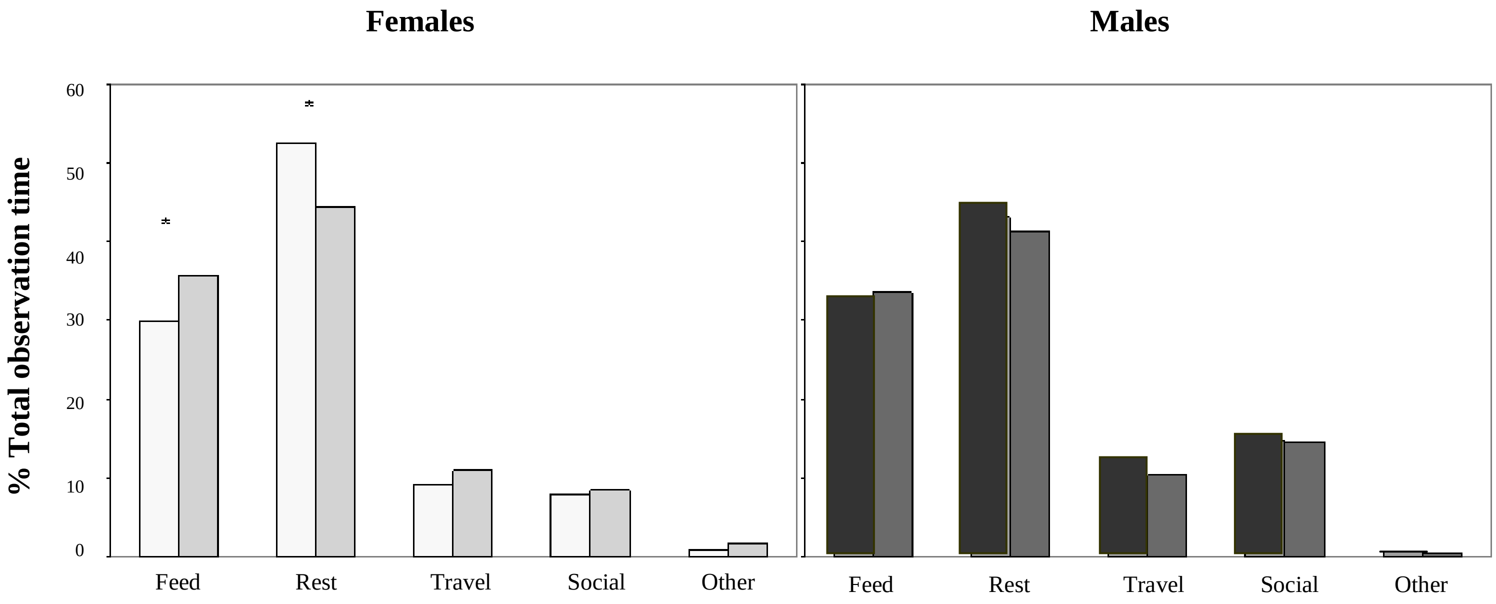
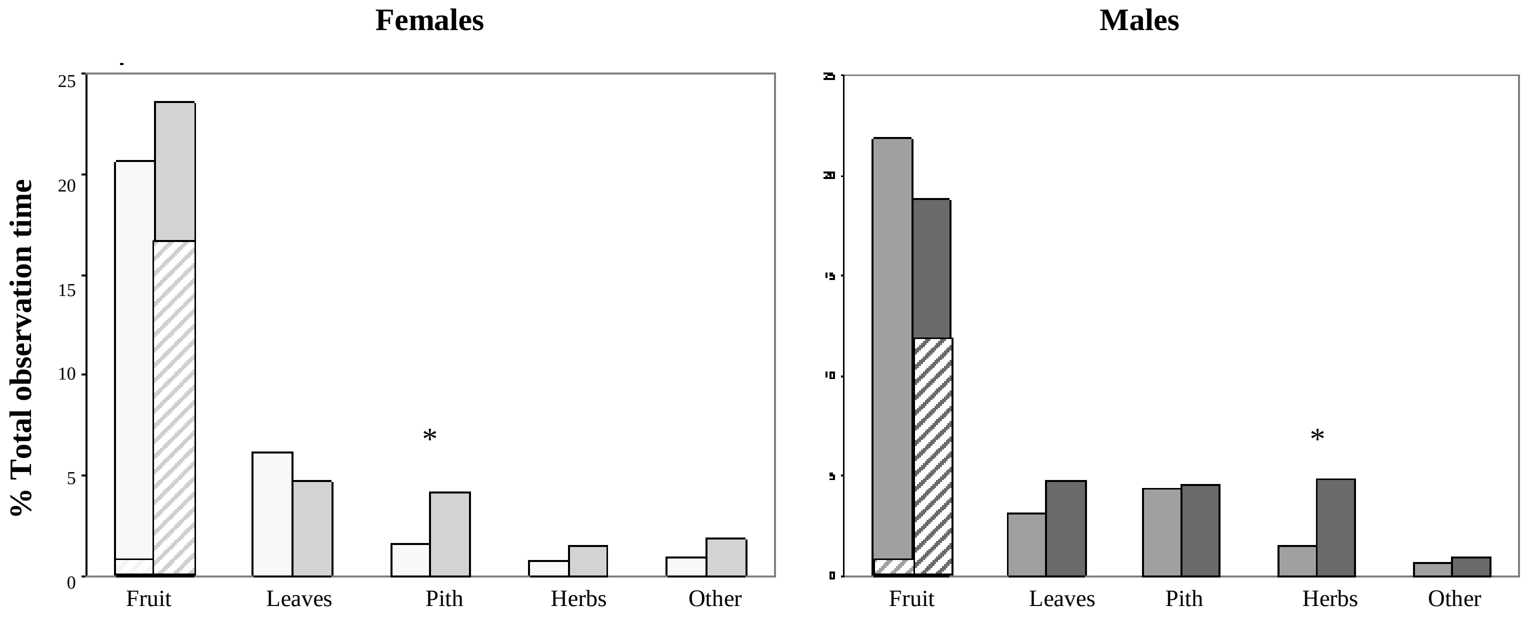


Figure 2.4 Seasonal variation in diet
For each sex, bars on the light bars on the left represent the NFF season and the dark bars on the right represent the FF season. Striped bars indicate the proportion of time spent feeding on fig fruit specifically.
* indicates significant difference at $p < 0.05$



Chapter 3

Compensating for competition: Do male and female chimpanzees (*Pan troglodytes*) differ in their response to scramble competition?

Abstract

In species characterized by fission-fusion grouping, individuals may modify group size based on social and ecological pressures, often resulting in sex differences in association and gregariousness. In chimpanzees (*Pan troglodytes*), females often travel in smaller parties and are less gregarious than males. This strategy is expected to allow females to better avoid the costs of feeding competition whereas males may be more likely to tolerate these costs in favor of social benefits. In this study I test the effects of party size separately in male and female chimpanzees in order to evaluate whether females effectively avoid costs of competition by spending more time in smaller parties. Full day follows were conducted over a period of 15 months on five focal females and five focal males in the Kanyawara community of Kibale National Park, Uganda. Standard proxies of scramble competition, including daily path length and feeding time, were recorded and estimates of energy expenditure and intake were calculated. Similar to previous studies, females in this community were found in smaller parties (7 individuals) than males (10 individuals). Females exhibited an increase in foraging costs, in the form

of increased travel expenditure, when in larger parties (Beta =0.38, p=0.02), whereas males did not (Beta= 0.25, p=0.28). However, females exhibited a positive relation between increased expenditure and energy intake in parties below 7 individuals indicating that they suffered costs only in larger parties. Males on the other hand showed little effect of party size constraints and consistently travelled in larger parties than females. The results of this study therefore provide the first quantitative evidence supporting the hypothesis that female chimpanzees forage in smaller parties than males in order to avoid costs of scramble competition.

Introduction

The influence of group size on feeding competition and social relationships has received much attention in socioecological studies. While group living affords certain benefits such as increased protection from predators (Pulliam 1973, van Schaik 1983), group size is ultimately constrained by the extent of intragroup feeding competition (Janson 1988, van Schaik 1989, Chapman 1990). The level of this competition is in turn dependent upon the size, distribution and availability of essential resources (Chapman and Chapman 2000). In the case of within group scramble competition (WGS), an increase in group size is expected to result in faster patch depletion and thus a decrease in the per capita intake of all group members (Janson 1988, Chapman and Chapman 2000). To compensate for this group size effect, individuals may be forced to travel farther in search of food, spend more time feeding on lower quality foods, and/or manipulate party size by increasing group spread or fissioning (Clutton Brock and Harvey 1977, Wrangham et al 1993, Janson and Goldsmith 1995). If this increased feeding effort does not result in a corresponding increase in intake, individuals are likely to suffer from WGS and reproductive success is expected to decrease.

Studies examining the nature of resource competition and group size in primates tend to focus on females since their reproductive fitness is more directly linked to access to food (Trivers 1972, Emlen and Oring 1977, Wrangham 1979a). While males are nonetheless vulnerable to group size effects, their reproductive success depends more on access to receptive females and they may thus benefit from remaining in larger groups (Altmann 1990). The effects of WGS are therefore expected to have a greater impact on female grouping and foraging behavior (van Schaik and van Noordwijk 1988, Koenig 2002). Although the costs of WGS are best measured based on patterns of net energy gain and relative reproductive success, increase in daily travel distance and time spent feeding are useful proxies to estimate foraging effort in relation to changes in party size (van Schaik et al 1983, Janson 1988, Koenig 2002). Based on these parameters, evidence suggests that both frugivorous and folivorous species often face WGS as resources become limited (long-tailed macaques: van Schaik and van Noordwijk 1988, chimpanzees: Chapman et al 1995, spider monkeys: Chapman et al. 1995, red colobus: Gillespie and Chapman 2001). However, few studies have directly compared the relative effects of party size in males and females. Since many primates live in cohesive groups in which males and females are limited in their ability to manipulate group size independent of each other, study of this problem is often difficult.

Chimpanzees (*Pan troglodytes*) provide an ideal opportunity to test the relative effects of group size on males and females due to their fission-fusion social organization. In fission-fusion, individuals belong to a permanent social group (community) with a shared home range, but travel and feed in subgroups (parties) that vary in composition and duration (Kummer 1971**,** Wrangham 1979a, Goodall 1986). In general, fruit patch size and availability as well as the presence of receptive females independently affect party size and composition, with larger parties forming in times of fruit abundance and female sexual receptivity (Goodall 1986**,** Matsumoto-Oda et al. 1998, Anderson et al. 2002, Mitani et al. 2002). When ripe fruit is limited, parties tend to be smaller and individuals resort to feeding in smaller patches or on lower quality fallback foods such as terrestrial pith and herbs (TPL) (Chapman et al. 1995, Newton-Fisher et al. 2000, Isabirye-Basuta 1989, Doran 1997, Murray et al. 2006 but see Anderson et al. 2002, Hashimoto et al. 2003, Itoh and Nishida 2007).

Across study sites, chimpanzee mothers are observed to spend more time alone or in small single-sex “nursery “ parties (Nishida 1979, Wrangham 1980, Goodall 1986, Doran 1997, Emery Thompson and Wrangham 2006, but see Boesch 1996). Males are typically found in larger parties, tend to be more social and form complex dominance hierarchies and coalitions that influence individual mating success and facilitate territorial defense and hunting (Wrangham 1979b, Constable et al. 2001, Boesch et al. 2006, Duffy et al. 2007). Presumably, this difference in gregariousness allows females to maximize foraging efficiency by reducing resource competition and travel costs as compared to males (Wrangham 1986, Wrangham 2000). However, support for this hypothesis is mixed. Studies show that both males and females spend less time feeding when in larger parties (Wrangham 1977, Wrangham and Smuts 1980, Pandolfi 2005). Yet despite the fact that females are often in smaller parties than males, these same studies show no sex difference in time spent feeding. While males are typically observed to range farther than females, the relationship between party size and daily travel distance within each sex is less clear. Some studies have found that only males travel farther when in larger parties (Wrangham and Smuts 1980, Chapman et al. 1995) while others suggest that mothers suffer higher costs when travelling in larger parties since they travel at slower velocities (Wrangham 2000, Williams et al. 2002a). In the Tai forest, where females are reported to be more gregarious in comparison to other sites, female daily path length was found to decrease whereas feeding time increased when in larger parties (Lehmann and Boesch 2004).

Such mixed results may be due to the confounding effects of party composition on party size. These may relate more to social aspects that are often difficult to quantify. For instance, mothers may favor all female groups, regardless of size, due to the benefits of infant socialization as well as avoidance of male aggression against offspring (Williams et al. 2002, Otali and Gilchrist 2006). Likewise, if female travel costs increase at a relatively higher rate than male travel costs due to a sex difference in velocity, forcing females to keep up when with males (Wrangham, 2000), this would imply that the number of males in a party rather than party size alone should limit females. Although less is known regarding the effects of male dominance on female foraging behavior, either through direct competition or priority of access, such factors may also influence female strategy (Wrangham 1979a, Smuts and Smuts 1993). It is therefore necessary to control for social composition in the analysis of party size in relation to feeding and travel.

In this study, I test effects of party size on males and females. I first assess whether males and females differ in party size and composition and whether this relation varies with fluctuations in preferred fruit availability. If females are more dependent on access to resources and less constrained by the need to be in a large party to obtain social benefits, it is predicted that they will be more likely to increase their party size in periods of greater fruit availability. Secondly, I test the hypothesis that females are more susceptible to costs of remaining in larger parties. As party size increases, both males and females are predicted to travel farther and spend more time feeding on lower quality items. However, this relation is expected to be stronger in females, particularly when in parties with more males. Finally, I test whether the sexes differ in compensating for these costs. If females are better able to adjust party size to avoid competition, it is predicted that they will join parties only when costs are matched by a corresponding increase in intake. If males are more likely to gain social benefits, I predict that they will join larger parties despite energetic costs. I test this prediction by examining whether increased travel or feeding effort result in increased intake. In order to distinguish the effects of party size as opposed to the effect of the number of individuals of the opposite sex in the party I examine these questions in terms of both party size and composition.

Methods

Study Site and Community

Research was conducted from May 2004 to July 2005 in the Kibale National Park located in western Uganda (Chapman et al. 1995, Struhsaker 1997). The majority of the 766 km^2, mid-altitude park is characterized by moist, evergreen forest and includes a mix of swamp, grassland, pine plantations, thicket, and secondary forest. Annual rainfall averages 1,662 mm, with two rainy seasons per year (typically March through May and August through November) (Struhsaker 1997).

This study focused on the Kanyawara community which has been the subject of long-term study by Dr. Richard Wrangham and the Kibale Chimpanzee Project (KCP) since 1987 (Wrangham et al. 1996). During the study period, the community consisted of 55 known individuals including 10 adult males (>16 years old), 3 adolescent males (8-15 years old), 14 adult females (> 14 years old) and 3 adolescent females (8-13 years old). Age classifications followed Goodall 1986 and were based on long-term birth records collected by the KCP.

Data Collection

Full day focal follows (Altmann 1974) were conducted on adult males and anestrous females (i.e. pregnant and lactating). Five individuals of varying rank and age were sampled from each sex in order to obtain a consistent and unbiased sample of the community throughout the study period. Each female traveled with at least one infant and one juvenile during the study. If a female focal animal came into estrus, she was not followed during the phase of maximal anogenital swelling (typically lasting 10-12 days (Goodall 1986)) in order to avoid confounding socio-sexual influences. All focal females exhibited similar levels of habituation and had previously been determined as “central” based on the fact that their core areas were found in the center of the community range (Emery Thompson et al. 2007). A field assistant was assigned to independently follow an individual to serve as a focal animal for the subsequent day in order to reduce the potential bias of following larger parties or individuals belonging to the same party for consecutive days. Although complete nest to nest follows were not always possible, the mean daily follow was 9.2 hours in duration.

Behavioral Data

During focal follows, activity (feeding, traveling, resting, social, and other) was recorded using one minute instantaneous sampling (Altmann 1974). Since different modes of travel have different energetic costs, travel was further classified as terrestrial quadrupedal walking, arboreal quadrupedal walking, climbing, or descending. Travel distance on the ground was measured continuously by pacing behind the focal animal. All arboreal travel distance was visually estimated. When the focal individual was feeding, the species and plant part were recorded. Intake rates were recorded opportunistically and measured as either the number of items (e.g. fruits, leaves) or the percentage of the food item ingested during a continuous 60 second interval. Patch size was measured for all fruit trees fed in by focal subjects as the diameter at breast height (DBH).

Focal animal party size and composition were recorded every 15 minutes with the help of a field assistant. Previous research at this site indicates that measures at this interval are independent and sufficient for monitoring changes in composition (Otali and Gilchrist 2006). Party size was defined as all adult and adolescent individuals within 50 meters of each other (50 meter chain rule Clark and Wrangham 1994. Parties were coded as: 1) alone (no other adults or adolescents, single sex (no other adults or adolescents of the opposite sex), or mixed sex (at least one other adult or adolescent of the opposite sex).

Ecological and Nutritional Data

Resource availability was defined based on the presence or absence of preferred non-fig fruit species in the diet. Long-term research indicates that chimpanzees of the Kanyawara community exhibit a clear preference for certain non-fig, or succulent drupe fruit species including *Mimusops bagshawei, Pseudospondias microcarpa,* and *Uvariopsis congensis* (Wrangham et al. 1996, Emery Thompson 2005). In a previous study at the same site, Sherry (2003) found that time spent feeding on preferred fruits was correlated with fruit availability. These species tend to fruit synchronously at the intraspecific level but asynchronously at the species level. This results in clear and isolated periods of preferred fruit availability during which these foods dominate the chimpanzee diet (Chapman et al. 1999). Figs, in contrast, are available year round but are unpredictable and scattered throughout the range (Chapman et al. 2005). Therefore, using similar methods to previous studies at this site (Emery Thompson 2005, Gilby and Wrangham 2007), the season was defined as non-fig fruit season if over 40% of the diet consisted of preferred fruit for three consecutive days. All other days were attributed to the fig fruit season. During the study period, the non-fig fruit season corresponded to two major periods including September to December and March to May.

Nutritional data for major foods eaten by the Kanyawara community (n=51 items covering 88% of total feeding time) were provided by Dr. Nancy-Lou Conklin-Brittain and Dr. Richard Wrangham of Harvard University (see Conklin-Brittain et al. 1998, Conklin-Brittain et al. 2006). Additional food items that were underrepresented or absent in the existing database were collected during this study (n= 29 items covering 5% of total feeding time). Samples were collected as close as possible to the location where an individual was observed feeding and transported back to the research camp. For each sample item (minimum of 10 samples per food item), the whole wet weight was recorded and the item was separated into component parts (e.g. seed, pulp, skin, peel, pith) before being dried in an onsite dryer, reweighed to the nearest gram, and stored for transport. Macronutrient analyses of newly collected items were conducted by the laboratory of Dr. Joerg Ganzhorn in the Department of Ecology and Conservation, Hamburg University. Methods used were comparable to those of Dr. Conklin-Brittain (Ganzhorn and Harthun 2000, Conklin-Brittain et al. 1998).

Energy content was calculated using standard physiological fuel values of 4 kcal/g carbohydrate, 4 kcal/g crude protein, and 9 kcal/g lipid based on human data (National Research 1980). Since chimpanzees may be able to extract additional energy from NDF through fermentation, an alternative measure of potential energy including fermentation was calculated using the physiological fuel value of 1.5kcal/g NDF (Milton and Demment 1988, Conklin and Wrangham 1994, Conklin Brittain et al. 2006).

Estimates of Travel Costs

Travel costs were measured in three ways: 1) time spent traveling, 2) daily travel distance, and 3) energetic expenditure due to locomotion. Time and distance traveled were included to allow for comparison with previous studies. Locomotor expenditure was estimated as a more accurate measurement of travel cost that compensates for energetic differences due to body size and reproduction. Time spent traveling was calculated as the total daily time spent in locomotion. In order to correct for possible sex differences in arboreality (Takemoto 2004), daily travel distance was defined as the total distance – both terrestrial and arboreal – covered in a day. Energy expenditure during locomotion was calculated as the sum of quadrupedal and vertical locomotion. For quadrupedal travel, I adapted the equation given by (Taylor et al. 1982) for primate locomotion:

$$\text{kcal}_{\text{walk}} = (0.0025 \text{ x } W^{0.702})\, D + (0.0017 \text{ x } W^{0.843})\, T$$

Where D is distance traveled in meters, T is time spent traveling in seconds, and W is weight in kilograms. I used Hanna's equation for the cost of transport during climbing since it was found that the mass specific cost of climbing remains constant across primates of different body mass (Hanna 2006):

$$\text{COT}_{\text{climb}} = (106.17)\,(W)^{-0.098}$$

where $\text{COT}_{\text{climb}}$ is measured in Joules kg^{-1} m^{-1}. The relation 1 Joule: 0.00024 kcal was used to convert energy expenditure to kilocalories. To calculate energy expended while descending a vertical support, I used the equation for potential energy

$$E_{PE} = W\ G\ D$$

where G is the force of gravity and D is distance traveled in meters. This was converted to metabolic energy by dividing by an efficiency of 95% and converting to kilocalories (Warren and Crompton 1998). Weights were based on (Smith and Jungers 1997) with a mean of 42.7kg for adult males and 33.7kg for adult females. The additional costs of pregnancy, lactation and infant transport were factored into expenditure calculations for females. Expenditure for pregnant and lactating individuals was multiplied by a factor of 1.25 and 1.5 respectively to compensate for increased costs of reproduction (Portman 1970, Oftedal 1984, Key and Ross 1999, Aiello and Key 2002). Infants were divided into three age categories (0-6mo, 7mo-2yr, 3-5yr) and weights were assigned based on previously estimated birth weights and growth trajectories (Zihlman 1997, Pusey et al. 2005). The proportion of time spent carrying an infant of a given class was calculated based on focal scans and the locomotor expenditure was adjusted for the added infant weight by multiplying by a constant (1.05, 1.15, and 1.30 respectively).

Intake and Feeding

Predictions of group size constraints differentiate between resources that are depletable and ones that are more evenly distributed (van Schaik and van Noordwijk 1988, Chapman and Chapman 2000). Time spent feeding was therefore calculated distinguishing between fruit and TPL feeding. Daily caloric intake was calculated as:

$$\text{Total intake} = \Sigma\,(T_i \times IR_i \times ENC_i)$$

Where T_i is the time spent feeding on food item *i* in minutes, IR_i is the average ingestion rate for food item *i* in grams per minute, and EC_i is the caloric content of food item *i*. , IR_i was calculated as the product of the average intake rate and the weight of food item *i*.

Analysis

Sex differences in party size and composition were examined using general linear models (GLM ANOVA). Changes in party size according to seasonal fruit availability were tested using a repeated measures design. Mean party size, percent time spent alone, percent time spent in single sex parties, and percent time spent in mixed parties were calculated per focal individual based on all 15 minute scan data (females: n= 2,657 scans, mean = 531.4 ± 32.7 scans per individual, males: n= 2,658 scans, mean = 532.3 ± 46.4 scans per individual).

The effects of party size on male and female travel, feeding, and intake were tested based on full day, nest to nest follows (n= 57, minimum of 5 follows per individual) using general linear models (GLM MANOVA). For each full day follow I calculated average daily measures of : 1) party size and party composition from 15 minute scan data, 2) percent time feeding on fruit, percent time feeding on TPL and percent time traveling from one minute instantaneous data, 3) locomotor expenditure (as described above) and 4) caloric intake (as described above). Daily follows were treated as independent (c.f. Knott 1998, Anderson et al. 2002, Fox et al. 2004). Although this approach introduces the possibility of pseudoreplication, all models included the focal individual as a random effect to test for variation (Baayen et al. 2002). The Durbin-Watson test for autocorrelation was used to test for sequential effects on residuals (Durbin and Watson 1971). The dependent variables, travel and feeding intake were each tested using three separate measures: travel: time spent traveling, daily travel distance and locomotor expenditure; feeding: time spent feeding on fruit, time spent feeding on TPL, and daily caloric intake. Average daily party size and composition (e.g. the number of males in the party and the number of females in the party), were entered as continuous predictors in separate analyses due to high correlation of party size measures. Season (categorical) and mean fruit tree DBH (continuous) were entered as independent predictors to control for effects of fruit availability. Colinearity of factors was examined using Spearman correlations. All data expressed as percentages and counts were transformed using the arcsin and log transformations respectively. Statistical analyses were performed using Statistica v. 5.5.

Results

Do males and females differ in party size and composition?

The mean party size for females (7 individuals) was smaller than that of males (10 individuals) (Table 3.1). Females had an average of 3.0 males and 3.9 females in their party whereas males had 6.8 males and 2.9 females in their party. The adult sex ratio of female parties did not differ from the expected ratio of 0.76 males: females based on community composition, whereas males were found in parties with more males than expected.

Females spent 18.3% of time alone (SD=14.9%, n= 5) compared to 6.6% (SD= 7.2%, n=5) for males, although this difference is not significant ($F_{(1,8)} = 2.518$, $p = 0.15$) (Table 3.2). The lack of statistical significance may be explained by the fact that two of the five focal females were often found in association with each other (65 and 88% of party scans respectively) and thus spent little time alone. Males spent more time in mixed parties (males: 75.9 ± 9.1% of time, n= 5, females: 46.1 ± 15.6% of time, n= 5, $F_{(1,8)} = 13.610$, $p < 0.01$) whereas females spent more time in single sex parties (males: 17.5 ± 5.8% of time, n= 5, females: 35.6 ± 14.3% of time, n= 5, $F_{(1,8)} = 6.846$, $p < 0.05$). Single sex parties were of similar size for both males and females (males: 3.9 ± 1.0, females: 3.1 ± 0.7, $F_{(1,8)} = 2.402$, $p = 0.16$), but males had larger party sizes than females when in mixed sex association (males: 11.5 ± 1.0, females: 9.3 ± 1.5, $F_{(1,8)} = 7.530$, $p < 0.05$).

Does party size change in relation to resource availability?

Males reduced their party size when preferred fruit was scarce (10.8 ± 1.2 vs. 8.8 ± 2.2, $F_{(1,4)} = 9.476$, $p < 0.05$) whereas female party size remained relatively constant across seasons (6.8 ± 1.1 vs. 7.1 ± 1.3, $F_{(1,4)} = 0.633$, $p = 0.47$). Although there was a tendency for male party size to increase with fruit patch size, this relation was not significant for either sex (males: $r = 0.189$, $p = 0.11$, females: $r = 0.061$, $p = 0.61$).

Do costs of party size differ between the sexes?

Females, but not males, travelled farther when in larger parties and this relation was true for all three estimates of travel (daily travel distance: Beta = 0.354, $p < 0.05$, travel time: Beta = 0.362, $p<0.05$, locomotor expenditure: Beta = 0.384, $p<0.05$) (Table 3.3a). In each case, for females, but not males, this result was combined with a significant inverse relationship between average daily fruit patch size and travel (Table 3.3a). When the analysis was repeated using party composition rather than size (e.g. using only the number of females or the number of males in the party as a factor), this significant relation in females was found to be primarily due to an increase in the number of females (Beta = 0.426, $p < 0.01$) in the party as opposed to an increase in the number of males (Beta = 0.262, $p = 0.12$).

For females, but not males, there was also a trend towards increased time spent feeding on fruit and TPL with increasing party size (fruit: Beta = 0.314, $p = 0.08$, TPL: Beta = 0.232, $p = 0.11$) (Table 3.3b). The relation of fruit feeding was also driven more by the effect of the number of females in the party (Beta = 0.318, $p = 0.07$) than males (Beta = 0.184, $p = 0.23$).

Do males and females compensate for increased effort?

A plot of female daily caloric intake against energy expenditure indicates that as daily travel expenditure increases, females initially compensate by increasing their daily calorie intake (Figure 3.1a). However a maximum of travel is reached beyond which females can no longer compensate and daily caloric intake begins to fall (quadratic: $\text{Beta}_1 = 6.852$, $\text{Beta}_2 = -1.407$, $p < 0.05$, linear: Beta= -0.144, $p=0.42$). When this is compared with the plot of the effect of mean party size on locomotor expenditure (as calculated above), results indicate that the peak of the energetic curve corresponds to a party size estimate of 7 individuals (Figure 3.1b). Similarly, the significant relation between female party composition and travel determined in the previous section predicted a female party size of 4 females corresponding to the peak of the energy balance curve. Although an increase in travel expenditure was negatively related to energy intake in males, this relation was not significant (Beta = -0.204, $p = 0.40$).

Daily feeding time was significantly positively correlated with caloric intake for males (Beta = 0.840, $p < 0.01$) but not females (Beta = 0.038, $p= 0.84$) (Figures 3.2a and b).

Discussion

The results of this study support the idea that female chimpanzees suffer greater foraging costs in larger parties compared to males and tend to vary their party membership accordingly. As party size increased, females, but not males, expended more energy in travel and tended to feed more. While previous studies have documented that females travel farther when in larger parties (Wrangham 2000, Williams et al. 2002a), this study demonstrates that larger party size results in reduced energetic gain for females. While males were found in larger parties overall, they did not suffer negative effects of competition as measured by the foraging parameters used in this study. This result contrasts with findings from Gombe where males were observed to travel farther and spend more time feeding in larger parties (Wrangham and Smuts 1980, Williams et al. 2002a).

Despite the potential costs, females spent the majority of their time in parties in which increased expenditure could be compensated with increased caloric intake. An initial increase in travel expenditure was correlated with an increase in intake. However, this relation only existed up to a certain point, after which further increase in expenditure ultimately led to a relative decrease in intake. The fact that females spent over 65% of their time in parties of less than or equal to this threshold value of 7 individuals suggests that, for the most part, they avoided significant costs of scramble competition. Nonetheless, females also spent a portion of their time in larger parties where they were more likely to suffer an energy deficit, suggesting that other factors such as social benefits influenced party membership. Although females also tended to increase the time they spent feeding on both fruit and TPL when in larger parties, this feeding time did not correspond to an increase in intake as was observed in males, and therefore may indicate a cost in terms of foraging effort. This most likely reflects differences in food selection as females in this study community were previously found to spend more time feeding on fallback foods that were nutritious but had a lower caloric return per unit feeding time (Chapter 2). Although females spent more time feeding on fig fruits when preferred fruits were scarce, these tended to give a low caloric return as compared to some of the herb species that constituted a larger part of the male diet (Chapter 2).

Although, in theory, resource competition is expected to be of greater importance for female reproduction, males are still expected to be subject to ecological constraints and party size pressures as well. Yet males in this study showed little response to changes in party size and composition. Recent research from Gombe suggests that males are more responsive to resource availability than previously assumed and may opt to forage alone and in familiar core areas when fruit is scarce (Murray et al. 2008). In accordance with this finding, males in this study reduced their party size in response to resource scarcity. While this change in party size did not lead to a decrease in social activity (Pokempner, unpublished data), it may nonetheless entail a social cost for males in terms of strengthening bonds and rank relations. It was previously found that males in this study group fed more on TPL when preferred fruit was low (Chapter 2), yet time spent feeding on TPL did not correlate with party size for males as it did for females. This result may indicate that an overall higher reliance on TPL allowed males to maintain larger parties than females, but that TPL feeding did not necessarily serve as buffer for variance in party size within males. Furthermore, the positive correlation found between feeding time and caloric intake suggests that, in general, males may have avoided competition in parties by feeding on foods with higher caloric intake rates.

The number of members of the opposite sex had little effect on the foraging behavior for both males and females. It has been suggested that females, particularly those with young infants, are expected to have higher travel costs when in parties since they travel at a slower velocity than males (Wrangham 2000, Williams 2002). An implication of this idea is that travel costs would be expected to increase at a higher rate when in the presence of more males. Contrary to this prediction, this study found that the number of females in the party had a stronger influence on female travel costs and feeding time. The lack of a response to the number of males in the party might indicate that females effectively avoided these potential costs by only joining parties with more males under conditions that would preclude increased travel, such as might be the case if fruit patches were large, abundant and clumped (c.f. Wrangham & Smuts 1980,Chapman and Chapman 2000). Female intake and feeding time was also unaffected by the number of males in the party, suggesting that intersexual food competition was not a major factor. Although this study did not fully address this aspect, more detailed research from Kibale and Budongo suggest that there is little difference in feeding efficiency in males and females when feeding in the same patch (Kahlenberg, 2006, Machanda pers comm).

While overall sex differences in party size and composition are similar to those reported at most East African chimpanzee study sites, females in this study were found to be relatively more gregarious than previously observed (Chapman et al. 1995, Wrangham 2002). Specifically, there were fewer observations of solitary females and a higher frequency of all female parties in comparison to former studies (Table 3.4a). The percentage of time females spent alone and in all female parties was in fact closer to recent values reported from Tai and Ngogo, as well as bonobos in Wamba, where females are observed to be more gregarious and form “cliques” (Pepper et al. 1999, Hohmann and Fruth. 2002, Lehmann and Boesch 2005, Wakefield 2008) (Table 3.4b). Females spent almost as much time in single sex parties as they did in mixed parties, suggesting that there may have been a benefit to remaining in parties with other females. Evidence from long term studies suggest that mothers may join other females in order to socialize juvenile offspring and to gain a buffer against male aggression (Goodall 1986, Williams et al 2002a, Otali and Gilchrist 2006). It is of note that the average size observed for all female parties corresponded to the optimal female party size as predicted by the intake/expenditure curve, suggesting that females were generally able to avoid costs of scramble competition in these parties. The discrepancy found between this current study and some of the previous studies, however, may in part be due to the bias of selecting a small sample of central females, two of which were frequent associates, as focal subjects. However, there is a clear distinction between peripheral and central females in terms of general gregariousness, range use and reproductive success, suggesting that it may be more appropriate to consider the behavioral strategies of these females separately (Williams et al. 2002b, Emery Thompson et al. 2007). In addition, although the females are habituated, they were often more difficult to follow for extended periods when alone and this may have introduced a bias.

An important factor not considered here is the impact of contest competition. Since contest competition results in variation in intake according to individual rank, this might confound interpretation of the effects of party size (Janson and van Schaik 1988, van Schaik and van Noordwijk 1988). While male chimpanzees have a clear dominance hierarchy, few studies have documented differences in individual intake (Pusey et al. 2005, Sherry and Ellison 2007). Similarly, while there is increasing support for contest competition effecting female strategy, evidence is primarily based on differential access to quality core areas, indicating that contest is likely to operate on a broader level (Pusey et al. 1997, Wittig and Boesch 2003, Murray et al. 2006, Emery Thompson et al., 2007). Although analyses in this study accounted for individual variation, I did not focus on the effects of dominance on relative intake. Likewise, the calculations of energy intake and expenditure used here relied upon standard estimates. While these estimates were consistent across sexes and thus should not affect comparative results, this generalization may have nonetheless obscured individual variation. In particular, individual ingestion rates were calculated as an average per individual-food item pairing. This study therefore does not address the possibility that individual feeding rates may vary over the course of a feeding bout or due to changes in feeding party size and composition (Chapman et al. 1995 but see Janson 1988, Whitten 1988).

The interaction between WGS and group size has been documented in a variety of primates (Koenig 2000, Gillespie and Chapman 2001, Saj and Sicotte 2007). However, studies of scramble competition have generally focused on overall group level effects or the impact on female relations (van Schaik and van Noordwijk 1988, Barton and Whiten 1993). The predominance of this focus is in part due to the fact that most primates live in cohesive groups and because theory predicts that resource competition should have a greater impact on female fitness. Yet, while little is known regarding sex differences in response to WGS, it is often invoked as a key factor influencing the sexually segregated grouping and ranging patterns observed in many fission-fusion species (chimpanzees: Wrangham 1986, kinkajous: Kays and Gittleman 2001, hyaenas: Smith et al 2008). In this study, I found that females suffered greater costs of increasing group size, particularly in terms of travel expenditure. While this reflects previous findings and models of chimpanzee social structure, the results presented here show that females can often avoid these costs through a corresponding increase in intake. While this result may be expected, it is perhaps more curious that males in this study show no effect of variation in party size. In the case of hyaenas, another fission-fusion species, Smith et al. (2008) concluded that competition impacts female hunting party size since per capita intake was observed to decrease in parties containing more individuals- however no comparison was made with males. Further research of the relative costs and benefits of grouping for males and females in other fission-fusion species is needed to better understand the social and ecological factors.

This is the first study to quantify the relation between party size and energetics in chimpanzees, and shows that females are more likely to suffer from resource competition in larger groups. This is a fundamental aspect of socioecological theory and is used to predict social and demographic patterns such as female dispersal and dominance regimes (Wrangham 1980, van Schaik 1989, Sterck et al. 1997). This study confirms that group size is indeed a major factor that influences resource competition in males and females differently.

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Table 3.1 Individual and mean party size and composition of males and females.

Results indicate comparison based on the mean value of each sex.

	Total Party Size		Number of Males		Number of Females	
	Mean	Range	Mean	Range	Mean	Range
AL	6.8	(1-19)	2.4	(0-12)	4.4	(1-9)
BL	6.6	(1-25)	2.7	(0-13)	3.9	(1-12)
NL	7.8	(1-21)	3.6	(0-13)	4.2	(1-8)
OU	8.1	(2-18)	4.1	(0-11)	4.0	(1-8)
TG	5.5	(1-21)	2.6	(0-12)	3.0	(1-9)
Female	**7.0 ± 5.1**	**(1-25)**	**3.0 ± 3.6**	**(0-13)**	**3.9 ± 2.1**	**(1-12)**
AJ	11.3	(2-23)	8.1	(1-13)	3.2	(0-10)
KK	8.4	(1-21)	5.9	(1-12)	2.5	(0-10)
LK	8.4	(1-22)	6.3	(1-13)	2.2	(0-9)
MS	11.2	(1-21)	7.1	(1-12)	4.1	(0-10)
YB	9.9	(1-20)	7.0	(1-13)	2.9	(0-9)
Male	**9.8 ± 5.3**	**(1-23)**	**6.8 ± 0.9**	**(1-13)**	**2.9 ± 3.4**	**(0-10)**
	$F_{(1,8)} = 12.326, p < 0.01$		$F_{(1,8)} = 53.896, p < 0.01$		$F_{(1,8)} = 6.405, p < 0.05$	

Table 3.2 Percent time observed in party association and mean party size for each major party type.

Figures show individual values and the mean value for each sex.

	Mixed		Same Sex		Alone	
	% Time	Party Size	% Time	Party Size	% Time	Party Size
AL	39.8	8.1	56.2	3.3	4.0	1
BL	32.9	11.0	38.9	3.2	28.2	1
NL	62.0	10.4	35.1	2.9	2.8	1
OU	63.7	9.6	16.6	3.9	19.6	1
TG	32.0	7.5	31.0	2.0	36.9	1
Female	**46.1 ± 5.8**	**9.3 ± 1.5**	**35.6 ± 174.3**	**3.1 ± 0.7**	**18.3 ± 14.9**	**1**
AJ	80.5	12.5	19.5	5.0	0	-
K	69.2	10.7	25.7	3.4	5.2	1
LK	73.1	10.2	17.5	4.8	9.4	1
MS	89.4	12.3	9.8	2.6	0.7	1
YB	67.3	11.9	15.2	3.8	17.5	1
Male	**75.9 ± 9.1**	**11.5 ± 1.0**	**17.5 ± 5.8**	**3.9 ± 1.0**	**6.6 ± 7.2**	**1**

Table 3.3a Results of general linear model examining effect of party size on indices of travel.

Full model parameters show best fit including all predictors. Independent effects shows effects of each predictor variable.

Travel Parameters		**Independent Effects**				**Full Model**			
		Party Size		**Patch Size**		**Model**			
		Beta	p	Beta	p	r2	df	F	p
Daily Travel Distance	Female	0.39	0.02	-0.64	0.01	0.55	7	4.11	0.00
	Male	0.29	0.17	0.01	0.96	0.36	7	1.37	0.28
Travel Time	Female	0.36	0.02	-0.67	0.01	0.57	7	4.46	0.01
	Male	0.17	0.45	0.15	0.52	0.23	7	0.74	0.64
Locomotor Expenditure	Female	0.38	0.02	-0.75	0.01	0.56	7	4.29	0.01
	Male	0.25	0.28	0.24	0.63	0.21	7	0.64	0.72

Table 3.3b Results of general linear model examining effects of party size on indices of feeding and intake.

Full model parameters show best fit including all predictors. Independent effects shows effects of each predictor variable.

Feeding Parameters		**Independent Effects**				**Full Model**			
		Party Size		**Patch Size**		**Model**			
		Beta	p	Beta	p	r2	df	F	p
Fruit Feeding Time	Female	0.31	0.08	0.30	0.13	0.40	7	2.29	0.06
	Male	0.06	0.82	-0.40	0.25	0.24	7	0.73	0.65
TPL Feeding Time	Female	0.28	0.11	0.02	0.93	0.60	7	5.16	0.19
	Male	-0.11	0.66	0.07	0.84	0.27	7	0.86	0.55
Caloric Intake	Female	-0.11	0.51	0.16	0.40	0.40	7	2.29	0.06
	Male	-0.14	0.43	-0.18	0.45	0.65	7	4.16	0.01

Table 3.4a Group composition in chimpanzees and bonobos.
Measures indicate percentage of **total party scans** observed in each party type for all individuals, **males and females combined**.

Site	Female Only	Male Only	Mixed	Solitary Female	Solitary Male
P. t. schweinfurthii					
Gombe[1]	9	8	49	24	10
Mahale[2]	13	11	52	32	-
Mahale[3]	17	9	63	2	9
Kanyawara[4]	5	17	51	18	2
Budongo[5]	11	8	68	6	4
Budongo[6]	12	9	74	3	3
P. t. verus					
Tai[7]	22	7	33	18	11
Tai[8]	18	20	52	-	6
Bossou[9]	49	-	42	10	0
P. paniscus					
Lomako[10]	21	8	69	2	2
This study	19	9	61	8	8

1 Williams et al 2002, 2 Nishida 1990, Takahata et al. 1996 Nishida et al. 2003, 3 Matsomoto-Oda et al. 1998, 4 Chapman et al. 1995, 5 Fawcett 2000, 6 Reynolds, 2005, 7 Doran 1997, 8 Boesch 1996, 9 Sakura 1994, 10 Hohmann and Fruth 2002

Table 3.4b Group composition in chimpanzees by sex.
Measures indicate percentage of total party scans observed in each party type calculated **for each sex, separately**.

Percentage of Total Party Scans Observed in Party Type

	Females			**Males**		
Site	Female only	Female mixed	Solitary Female	Male only	Male mixed	Solitary male
P. t. schweinfurthii						
Gombe[1]			44			14
Gombe[2]			65			27
Mahale[3]			10			50
Ngogo[4]	20	56	20			
P. t. verus						
Tai[5]	19	18	45	18	44	26
Tai[6]		82	4		74	
Tai[7]	40	41	19		71	
This study	36	46	18	18	76	7

1 Murray et al 2006, 2008, 2 Wrangham and Smuts 1980, 3 Matsomoto-Oda et al. 1998, 4 Wakefield 2008, 5 Doran 1997, 6 Boesch 1996, 7 Lehmann and Boesch 2008

Figure 3.1 Plots of the relationship between locomotor expenditure and a) caloric intake and b) mean daily party size in females.

In both a and b the x axis, log daily locomotor energetic expenditure, is the same. The relationship between party size and expenditure predicts a party size of 7 individuals.

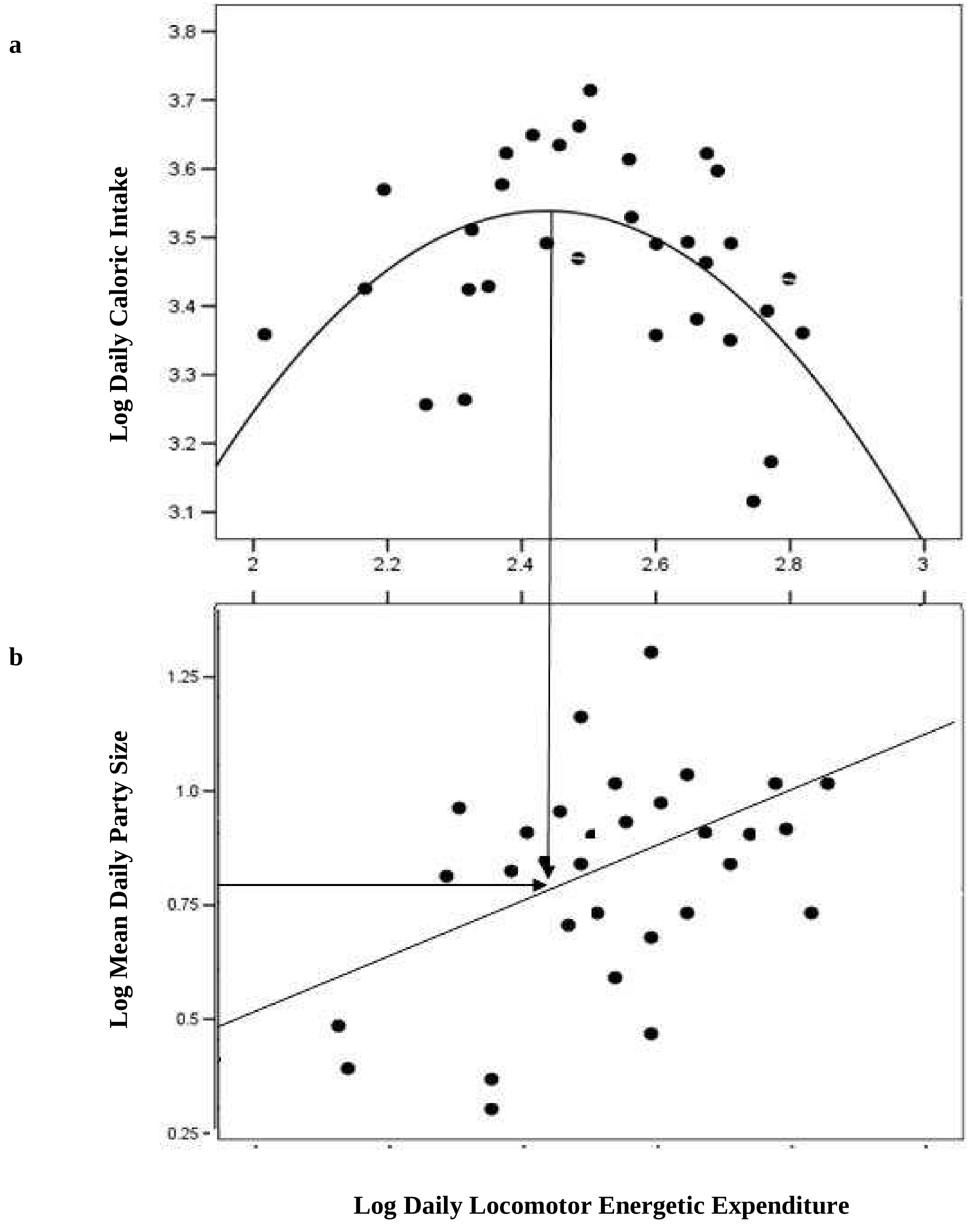
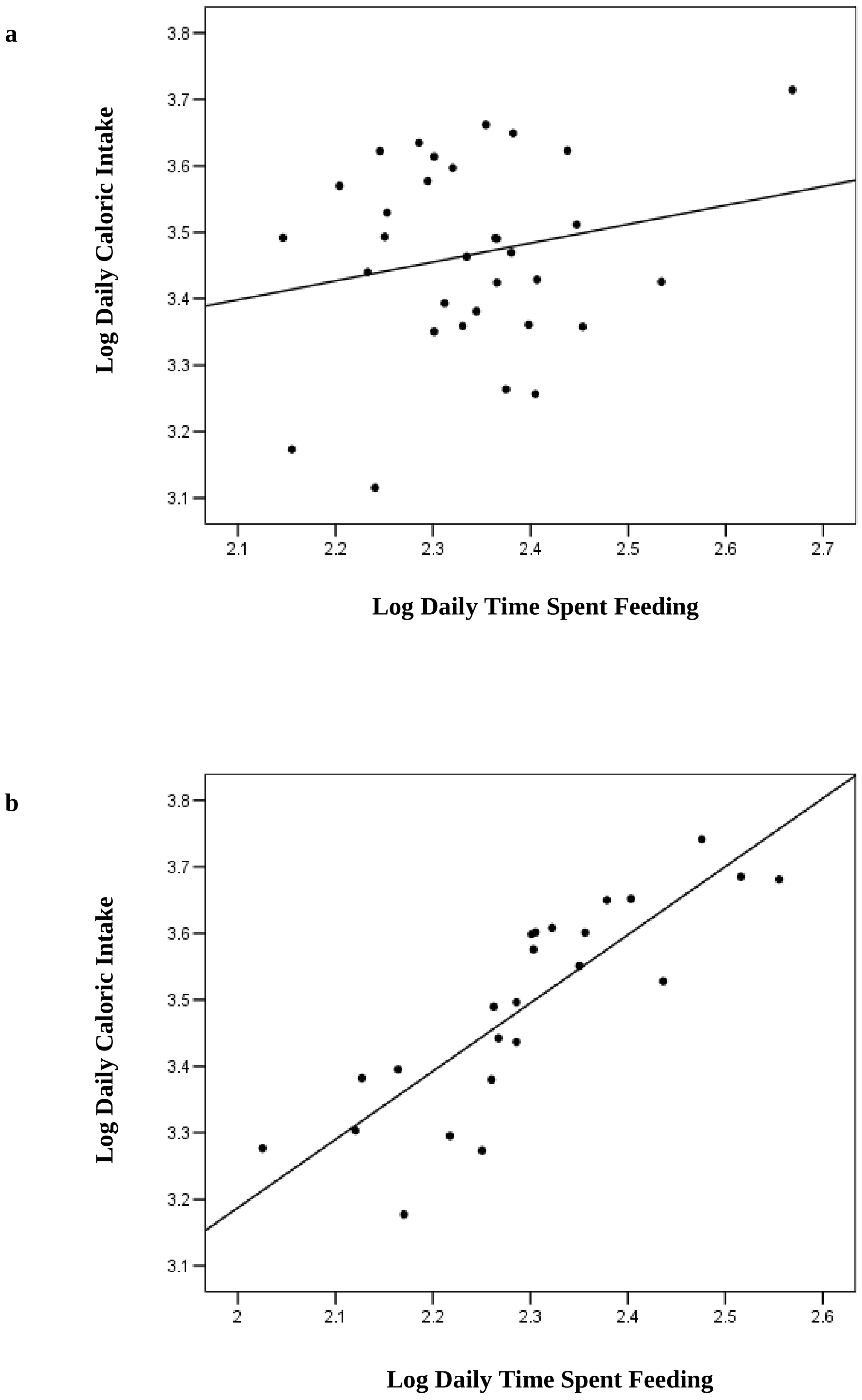


Figure 3.2 Plots of the relationship between daily feeding time and caloric intake in a) females and b) males.



Chapter 4

Do sex differences in range use in chimpanzees (*Pan troglodytes*) reflect greater foraging effort in females?

Abstract

The sex difference observed in ranging patterns among most populations of chimpanzees (*Pan troglodytes*) is often attributed to the fundamental difference in reproductive effort between the sexes. Among mammals, males are expected to range so as to maximize access to receptive females, whereas female ranging is expected to reflect greater access to food resources in order to maximize reproductive fitness. Although there is variation among study sites, observations seem to support this idea, with chimpanzee males tending to travel farther and using larger home ranges as compared to females. However, while these general patterns of home range size have been well documented, few studies have examined the relation between range use, individual movements, and foraging among the sexes in order to test whether these relationships conform to theoretical predictions. In this study I investigate whether sex differences in ranging reflect differences in foraging strategy among male and female chimpanzees by examining how travel and home range use relate to patch use and fruit availability. Full day follows were collected over a period of 15 months on five focal females and five focal males in the Kanyawara community of Kibale National Park, Uganda. Daily travel distance and range size were recorded in relation to parameters including patch size, number of patches visited per day, inter-patch distance, and fruit availability. While both males and female visited the same number of food patches per day, females did so by using a smaller range which they used more intensively, covering a greater proportion of their range on a daily basis. Females also responded to resource availability more by significantly expanding their home range area during periods of preferred fruit scarcity as compared to males In contrast to previous findings, total daily travel distance was similar for both sexes when both arboreal and terrestrial travel were considered (females: 2.3km, males: 2.8km). Females however tended to travel shorter distances between food patches (females: 370m, males: 443m, $p=0.06$) and did so in a more linear fashion as compared to males ($p < 0.02$). Overall, these results support the hypothesis that sex differences in ranging in chimpanzees reflect greater foraging effort in females, with female travel and range use responding more to resource availability and distribution.

Introduction

Variation in range use among mammals is influenced by a number of factors including body size (McNab1963, Milton and May 1976), predation (Swihart et al. 1988), territoriality (Mitani and Rodman 1979, Grant et al. 1992, Lowen and Dunbar 1994,) and the availability of food and non-food resources (Altmann 1974, Gompper and Gittleman 1991). Within a species, sex differences in ranging are often attributed to differences in reproductive priorities (Clutton-Brock and Harvey 1978, Sandell 1989). Female reproductive success is limited by energetic intake, while male reproductive success primarily depends on access to receptive females (Trivers 1972, Emlen and Oring 1977). Females are therefore expected to range so as to maximize access to food resources whereas male range use is expected to reflect greater mating effort through mate defense or resource defense (Mace and Harvey 1983, Wrangham 1987, Clutton-Brock 1989). Evidence for this idea is found in a variety of species, particularly those in which individuals are largely solitary or sexually segregated. In such cases, males defend a larger range containing those of dispersed females (leopard: Mizutani and Jewell 1998, wallabies: Fisher and Lara 1999, Iriomote cat: Schmidt et al. 2003), male range use responds primarily to female distribution (eastern gray squirrel: Kenward 1985, voles: Ims 1987, yellow-bellied marmots: Salsbury and Armitage 1994, Nelson 1995, black bear: Powell et al. 1997) and female range use responds to food availability (bobcat: Litvaitis et al.1986, roe deer: Tufto et al. 1996, black bear: Powell et al. 1997).

Chimpanzees (*Pan troglodytes*), however, are exceptional among primates in that they exhibit sex differences in ranging patterns despite being social foragers (Watts 2005). Chimpanzees are characterized by a fission-fusion social system in which individuals belong to a permanent multi-male, multi-female social group (community) with a shared home range, but travel in subgroups (parties) that vary in composition and duration (Kummer 1971**,** Wrangham 1979a, Goodall 1986). Anestrous females are typically less social than males, spending more time alone and in smaller parties, presumably to avoid resource competition (Nishida 1979, Wrangham 1980, Goodall 1986, Doran 1997, Emery Thompson and Wrangham 2006, but see Boesch 1996). Females often avoid peripheral areas of the community and concentrate their activities in smaller core areas which may form distinct neighborhoods (Gombe: Wrangham and

Smuts 1980, Goodall 1986, Williams et al 2002b; Mahale: Hasegawa 1990; Kibale: Chapman and Wrangham 1993, Wilson 2001 but see Lehmann and Boesch 2005). In contrast, males are more gregarious and are often observed to travel at faster speeds and in larger parties than females (Wrangham and Smuts 1980, Goodall 1986, Willams et al. 2002a). Males, the philopatric sex, also cooperatively and aggressively defend the community territory through patrols and lethal intergroup encounters (Wrangham 1979a, Smuts and Smuts 1993, Watts and Mitani 2001, Williams et al. 2004). As a result, males typically travel longer distances and use larger, overlapping home ranges whereas anestrous females travel shorter daily distances and use smaller home ranges dispersed within the community range (Wrangham and Smuts 1980, Chapman and Wrangham 1993, Doran 1997, Williams et al. 2002b).

In general, long-term studies indicate that the sex differences observed in chimpanzee ranging patterns are linked to reproductive benefits. Watts and Mitani (2001) have shown that individual males who frequently participate in boundary patrols are characterized by greater mating success. It has also been suggested that males benefit from territoriality by excluding unrelated males from both mate and food competition (Manson and Wrangham 1991, Wilson and Wrangham 2003) and providing greater resource availability to resident females, thereby increasing female fecundity, and ultimately their own (male) reproductive fitness (Williams et al. 2004). Space use in males is therefore often described in relation to social and mating benefits.

For females, reproductive fitness and rank vary with the location, quality and size of their core area. Females found in smaller, high quality areas have shorter interbirth intervals and higher infant survival rates than lower ranking females who are often characterized by larger, lower quality areas found near the periphery of the group range (Nishida 1989, Pusey et al. 1997, Williams et al. 2002, Murray et al. 2007, Emery Thompson et al. 2007). These studies imply that female core area use affords greater familiarity with and access to available resources within the range (Williams et al.2002, Murray et al. 2007, Emery Thompson et al. 2007).

The theoretical construct linking the conflict in reproductive priorities to range use is therefore well supported among chimpanzees. By extension, it also predicts how various components of foraging behavior should differ between the sexes. Yet despite a wealth of data on long-term ranging patterns, there is little evidence linking sex differences in range use to more proximate measures of foraging. Chimpanzees are ripe fruit specialists and supplement their diet with fallback foods such as leaves, figs, and terrestrial pith and leaves (TPL) when preferred fruit is scarce (Wrangham 1977, Wrangham et al. 1996, Conklin-Brittain et al. 1998). Due to the flexibility of fission-fusion grouping, there is a complex relation among party size, travel and ecological constraints such as the distribution, availability and size of fruit patches (Isabirye-Basuta 1989, Isbell et al. 1998, Chapman and Chapman 2000). Chimpanzees therefore illustrate many of the basic relations outlined in foraging theory and the ecological constraints model (Chapman and Chapman 2000). As party size increases group members must either travel farther and feed in more food patches, visit larger patches, or switch to lower quality but more abundant resources in order to compensate for increased feeding competition, particularly during periods when preferred fruit is scarce (Wrangham et al. 1993, Chapman et al. 1995, Chapman and Chapman 2000). In some cases, home range size expands during periods of lower fruit availability when individuals rely more on scattered foods (Basabose 2005, Murray 2007). Alternatively, home range has also been observed to contract when fruit is scarce and individuals supplement their diet with more leaves and herbs (Wrangham 1977, Hasegawa 1990, Doran 1997, Lehmann and Boesch 2003). However, few studies have looked more specifically at these patterns in terms of sex differences with the exception of Wrangham and Smuts (1980) who found that large resources used by females were closer together than those used by males. In studies of spider monkeys, which are also characterized by fission-fusion, individuals were observed to travel in rather linear and regular routes between fruit patches (DiFiore and Suarez 2007, Valero and Byrne 2007). While the former study concentrated only on females, the latter found no significant sex difference (DiFiore and Suarez 2007, Valero and Byrne 2007). In addition, van Roosmalen (1985) observed that female spider monkeys had a detailed knowledge of fruit resources in their core area. Thus, while sex differences in ranging are proposed to be derived in part from a conflict in reproductive and foraging investment, there is little known about how these fission-fusion spatial patterns are related to sex differences in foraging.

In this study I test the hypothesis that female range use is more closely related to foraging than male range use by examining specific movement patterns in relation to foraging in the Kanyawara chimpanzee community. Aureli et al. (2008) proposed that dynamics of fission-fusion are best examined by testing for deviations from a null foraging model in which all individual decisions of ranging and grouping are based on maximizing access to resources. Using this framework, if female ranging is more linked to foraging, then they are expected to conform to the null model and adapt their ranging to ecological constraints. Males, in contrast, are expected to deviate from the null model if social factors have a greater impact on their ranging patterns. I examine this prediction by first establishing whether males travel farther and use larger home ranges than females as has been found in previous studies of eastern chimpanzees. Next, I test how strongly male and female travel patterns are related to resource availability. More specifically, if female travel is linked more to foraging, I predict that daily travel distance will be positively related to the number of fruit patches visited per day and negatively related to the average size of fruit patches visited per day when party size effects among males and females are controlled for. Likewise, if females are more likely to maximize foraging effort, then it is expected they will do so in part by using their range in a more efficient manner. It is therefore predicted that females will travel more efficiently between fruit patches, using shorter distances and more linear routes. Females are also expected to use their range in a more clumped fashion and to cover their range more intensively than males. Given that females in this study group were previously found to depend more on fig fruit as a fallback food, whereas males preferred TPL (Chapter 2), I predict that female range size will vary more with preferred fruit availability.

Methods

Study Site and Community

Research was conducted from May 2004 to July 2005 in the Kibale National Park located in western Uganda (Chapman et al. 1995). The majority of the 766 km^2, mid-altitude park is characterized by moist, evergreen forest and includes a mix of swamp, grassland, pine plantations, thicket, and secondary forest. Annual rainfall averages 1,662 mm, with two rainy seasons per year (typically March through May and August through November) (Struhsaker 1997).

This study focused on the Kanyawara community which has been the subject of long-term study by Dr. Richard Wrangham and the Kibale Chimpanzee Project (KCP) since 1987 (Wrangham et al. 1996). During the study period, the community consisted of 55 known individuals including 10 adult males (>16 years old), 3 adolescent males (8-15 years old), 14 adult females (> 14 years old) and 3 adolescent females (8-13 years old). Age classifications followed Goodall 1986 and were based on long-term birth records collected by the KCP.

Data Collection

Full day focal follows (Altmann 1974) were conducted on adult males and anestrous females. Five individuals of varying rank and age were sampled from each sex in order to obtain a consistent and unbiased sample of the community throughout the study period. Each female traveled with at least one infant and one juvenile during the study. If a female focal animal came into estrus, she was not followed during the phase of maximal anogenital swelling (typically lasting 10-12 days (Goodall 1986)) in order to avoid confounding socio-sexual influences. All focal females exhibited similar levels of habituation and had previously been determined as “central” based on location of core area within the community range (Emery Thompson et al. 2007). A field assistant was assigned to independently follow an individual to serve as a focal animal for the subsequent day in order to reduce the potential bias of following larger parties or individuals belonging to the same party for consecutive days. Although complete nest to nest follows were not always possible, the mean daily follow was 9.2 hours in duration. While no patrols, as defined by Watts and Mitani (2001) occurred on the focal follow days included in this study, the chimpanzees nonetheless visited extreme points within their known range.

Travel distance was measured continuously by pacing behind the focal individual (Isbell et al. 1999). Arboreal travel distance was estimated and consisted of vertical travel up and down trees as well as all travel within the canopy. The location of the focal individual was recorded every fifteen minutes using a handheld Global Positioning System (GPS) unit (Garmin 12XL; error <10m). Additionally, the location of all food patches, including 1) fruit patches (fig and non-fig fruit), 2) terrestrial herbaceous pith and leaves (TPL), and 3) tree leaves, visited by the focal subject was recorded using the GPS.

For most fruit and leaf species, a patch was equivalent to an individual feeding tree and was measured as the diameter at breast height (DBH). In some species (i.e. *Mimusops bagshawei, Uvariopsis congensis*), fruit trees were often clustered in groves allowing individuals to feed consecutively in these trees without extensive travel. In such cases, a patch was defined as fruit trees of the same species that were within 20m of each other and the patch was estimated as the sum of the DBH measurements for each of the trees that the focal individual visited. TPL can be encountered either as isolated stems scattered throughout the forest or in larger, concentrated fields of vegetation. For the purposes of this study, a TPL patch was defined as any patch greater than 2 x 2m.

Analysis

Daily Travel Distance

In previous studies of chimpanzee daily path length (DPL) and day journey length (DJL) are typically based on the cumulative straight line distances travelled between successive location points recorded at standard 15 or 30min intervals (Wrangham and Smuts 1980, Herbinger et al. 2001, Williams et al. 2002, Lehmann and Boesch 2004, Pontzer and Wrangham 2004 but see Doran 1997). As a result, they may underestimate total travel since they fail to take into account travel within resources, meandering travel between resources and travel that occurs in trees. This method could potentially lead to sex-related biases in the measurement of travel if one sex travels more within resources, in a less linear fashion between resources or, as has been reported for chimpanzees, is more frequently arboreal (Takemoto 2004). To prevent these potential sources of error, I calculated daily travel distance (DTD) as the sum of all terrestrial and arboreal travel during nest to nest follows (n=60) (Table 4.1). Time spent arboreal and terrestrial was calculated as the percentage of total observation time observed in each category.

Home Range

Home range size was calculated from all 15min location points recorded during focal follow days (n= 149 days) using both the minimum convex polygon (MCP) and grid cell methods (Mohr 1947). The MCP home range was calculated as the smallest polygon encompassing 100%, 99%, 98%, 95% and 90% of all GPS points in order to test for the effects of outliers. Since there was no significant difference in home range estimate according to the percentage of points used ($F_{1,4}$= 2.131, p=0.20), I present the values using 98% of points in this paper. I calculated home range with the grid cell method by overlaying a 500 x 500m grid over the study area, determining the number of grid cells entered by the focal individual, and multiplying by the total by the area of each grid cell (0.25km^2). Although both methods have reported weaknesses, specifically the MCP method tends to overestimate range size due to sensitivity to sample size and outliers and the accuracy of the grid cell method depends upon the grid cell size (Powell 2000), they are both commonly used in primate studies, and therefore used here to permit comparison with previous work (Newton-Fisher 2003, Lehmann and Boesch 2005). In order to test whether sample size was sufficient and comparable, I calculated area curves for each focal individual. A plateau in range size was reached for each individual (mean plateau at 330 location points). Since sample size for each individual was greater than 330 points (Table 4.1), this suggests an accurate measure of home range size was measured for each individual. All spatial analysis was conducted using the Biotas v. 1.3 software (Ecological solutions 2005).

Patch Use

Travel between feeding patches, i.e. inter-patch travel, was calculated as the total distance (terrestrial and arboreal) travelled between leaving one feeding patch and entering the subsequent one. Inter-patch travel was categorized more specifically as 1) travel between all patches (fruit, leaf and TPL) and 2) travel between fruit patches. GPS location points of food patches were entered into Biotas and the straight line distance between feeding patches was determined. To test whether males and females differed in how directly they travelled between patches I calculated an inter-patch linearity index as the ratio between the straight line distance and the actual distance travelled between patches following Valero and Byrne (2007). Thus, the higher the ratio (approaching 1), the more directly chimpanzees travelled between patches. Each inter-patch segment was treated as a data point (females: inter-patch n= 306, linearity n= 150; males: inter-patch n= 284, linearity n= 149).

Home Range Use

To examine how uniformly males and females used their home range, I calculated the standardized Morisita index of dispersion for each individual (Krebs 1999). The index ranges from -1.0 to +1.0, and measures relative grid usage, with indices above zero indicating a clumped pattern, indices below zero indicate a uniform pattern and an index of zero denoting a random pattern of aggregation of location points. This index has the advantage of being independent of density and sample size, but may be sensitive to quadrat size (Myers 1978, Lehmann and Boesch 2005).

The intensity of home range usage was calculated using two metrics based on daily travel measurements. First, for each individual, the intensity of movement was calculated as the DTD divided by the square root of the home range (Goszczynski 1986 as adapted by Loretto and Viera 2005). This measurement describes to what extent the individual covers its home range in a given day. Secondly, I evaluated the degree to which each sex used its total home range on a daily basis by calculating the percentage of daily home range to total home range (Schmidt et al. 2003). Both parameters allow for evaluation of home range used on finer scale of daily foraging activity.

Seasonal variation in range use was investigated by distinguishing between the fig fruit and non-fig fruit season. Long-term research indicates that chimpanzees of the Kanyawara community exhibit a clear preference for certain non-fig, or succulent drupe fruit species including *Mimusops bagshawei, Pseudospondias microcarpa,* and *Uvariopsis congensis* (Wrangham et al. 1996, Emery Thompson 2005). In a previous study at the same site, Sherry (2003) found that time spent feeding on preferred fruits was correlated with fruit availability as measured by phenological transects. These species tend to fruit synchronously at the intraspecific level but asynchronously at the species level. This results in clear and isolated periods of preferred fruit availability during which these foods dominate the chimpanzee diet (Chapman et al. 1999). Figs, in contrast, are available year round but are unpredictable and scattered throughout the range (Chapman et al. 2005). Therefore, using similar methods to previous studies at this site (Emery Thompson 2005, Gilby and Wrangham 2007), the season was defined as non-fig fruit season if over 40% of the diet consisted of preferred fruit for three consecutive days. All other days were attributed to the fig fruit season. During the study period, the non-fig fruit season corresponded to two major periods including September to December and March to May. Individuals and sexes were sampled evenly across seasons.

Statistics

General linear models (GLMs) were used to evaluate sex differences in ranging parameters. Each focal individual was treated as an independent data point unless otherwise indicated (i.e. inter-patch travel analysis). Analyses of seasonal variation used a repeated measures design to account for repeated sampling of the same individual. The relationship between DTD and foraging parameters was also evaluated using GLMs. For this analysis, each complete full day follow was treated as an independent data point (c.f. Knott 1998, Anderson et al. 2002, Fox et al. 2004). Although this approach introduces the possibility of pseudoreplication, the model included the focal individual as a random effect to test for variation (Baayen et al. 2002). DTD was entered as the dependent variable and mean daily fruit patch size and the total number of fruit patches visited per day were entered as continuous predictor variables. Since previous studies have shown effects of party size and season on DTD, these factors served as covariates to control for effects (see Chapter 3 for methods regarding party size). Partial correlation analysis was used to investigate the variance in DTD attributed to each of the test variables after controlling for the effects of the other independent variables. All data not meeting the assumptions of the normal distribution were log transformed. Statistical analyses were performed using Statistica v. 5.5.

Results

Sex Differences in DTD and Home Range Size

In contrast to previous studies (Wrangham 1979b, Williams et al. 2002b, Pontzer and Wrangham 2004), there was no significant difference in total daily travel distance between males and females, with females traveling on average 2.3 ± 0.5 km and males traveling 2.8 ± 0.5 km per day ($F_{(1, 4)}$=1.810, p=0.22) (Table 4.1). While males tended to travel farther on the ground (females: 1.8 ± 0.5 km, males: 2.4 ± 0.5 km, $F_{(1, 4)}$=3.362, p=0.10), females travelled farther in the trees (females: 486 ± 71 m, males: 393 ± 60 m, $F_{(1, 4)}$=5.080, p=0.04). Greater arboreal travel in females is not unexpected given that females spent significantly more time arboreal compared to males (females: 73% of time arboreal vs. males: 40% of time arboreal, $F_{(1, 4)}= 42.037$, $p<0.01$).

Males used larger home ranges than females regardless of the method used to calculate home range size (98% MCP: females: 5.9 ± 1.0 km^2, males: 11.7 ± 1.3 km^2. $F_{(1, 4)}= 100.50$, p= 0.00; grid cell: females: 6.2 ± 1.6 km2, males: 9.5 ± 1.1km^2, $F_{(1, 4)}= 61.442$, $p<0.01$) (Figure 4.1).

Travel Distance in Relation to Foraging

In order to compare the relative relationship between travel distance and patch use, I first examined whether there was a sex difference in overall patch use. Males and females did not differ in the total number of food patches visited per day. Both visited an average of six food patches per day (females 5.8 ± 0.9 patches, males 6.2 ± 1.0 patches, $F_{(1, 4)}= 0.364$, p=0.56), four of which were fruit (females: 3.7 ± 0.5 patches, males: 3.9 ± 0.9 patches, $F_{(1, 4)}= 0.421$, p= 0.54). The average size of fruit patches, including groves, visited per day by males and females also did not differ (mean DBH females: 123.5 ±12.2 cm, males: 106.9 ± 22.7cm, $F_{(1, 4)}=2.092$, p=0.19).

Next I tested whether both male and female ranging patterns were equally based on maximizing access to resources as predicted by the null foraging model, or conversely whether female ranging was influenced more by foraging. For both sexes the daily travel distance was predicted by the number of fruit patches visited as would be expected if ranging was tied to foraging efficiency (females: partial r = 0.38, p=0.01, males: partial r = 0.29, p=0.01) (Table 4.2). However, a second foraging indicator, mean patch size, predicted female but not male travel, since female travel decreased with increasing patch size (females: partial r= -0.53, p= 0.05, males: partial r= -0.46, p=0.40) (Table 4.2). When either all patches or only fruit patches were considered, females travelled shorter inter-patch distances than males (Table 4.3), although this was only a trend towards significance in the latter case. Females also travelled more directly between fruit patches than males, with a linearity of travel index of 0.8 versus 0.74 (Table 4.3). Females did not travel more directly than males when travel between all patches was considered (Table 4.3).

Home Range Use

Both males and females exhibited standardized Morisita indices greater than zero, indicating that they both used their range in a clumped fashion. However, this was more the case in females who used their range in a more clumped distribution (females: 0.54 ± 0.01, males: 0.52 ± 0.00, $F_{(1, 4)}$= 6.808, p= 0.04).

Males tended to use a larger daily home range than females (females: 0.062 ± 0.01km^2, males: 0.08 ± 0.02 km^2, $F_{(1, 4)}$= 4.334, p=0.07) (Table 4.4). Females were thus able to cover their own home range more intensively on a daily basis – both in terms of the actual distance covered (females: 0.92 ± 0.14, males: 0.74 ± 0.14, $F_{(1, 4)}$= 5.728, p=0.04) as well as the percentage of total home range area (females: 1.00 ± 0.16%, males: 0.81 ± 0.14%, $F_{(1, 4)}$= 4.302, p=0.07) (Table 4.4).

Both males and females increased the size of their home range when preferred fruit was scarce however this difference was only significant in females (females: 4.84 ± 2.06 vs. 1.99 ± 1.47 km^2, $F_{(1, 8)}$= 9.735, p=0.04, males: 8.15 ± 2.37 vs. .53 ± 1.99 km^2, $F_{(1,}$

$_{8)}$= 3.872, p=0.12) . Despite this change, males tended to maintain a larger home range in both seasons (Table 4.5)

Discussion

Travel Distance and Range Size

Similar to previous studies of eastern chimpanzees, this study found that males use a larger home range than females (Wrangham 1977, Wrangham and Smuts 1980, Hasegawa 1990, Williams et al. 2002b). However, in contrast to these same studies, total travel distance was similar for both sexes. If only terrestrial travel- an approximation of straight-line distance- is considered, males tended to travel greater distances that are in fact similar to those reported in a previous study at this site using different methods (Pontzer and Wrangham 2004) (Table 6). While it is widely recognized that female chimpanzees are more arboreal than males (Wrangham and Smuts 1980, Hunt 1989, Doran 1993, Takemoto 2004), this factor has not been previously considered in measures of travel distance. By including all travel in the measure of DTD, this study accounts for this discrepancy and reveals that the addition of female travel in the canopy, both between and within food patches, may reduce the perceived sex difference that results when only straight-line or terrestrial travel is recorded. It is of note that at Tai, where males and females are most similar in terms of time spent arboreal, the sexes are also observed to travel similar distances (Herbinger et al. 2001) (Table 6). This lack of a sex difference is perhaps most relevant when considering the comparative locomotor costs for the sexes as this finding would imply that differences in ranging are not necessarily due to different strategies of energy conservation. Given that chimpanzee mothers may have greater energetic costs than males due to reproduction, this result suggests that females in this community are, on average, expending more energy on travel than males (Key and Ross 1999, Chapter 2). If this prediction is tested using calculations outlined in Chapters 2 and 3, females in fact tend to expend more energy than males in travel (364 versus 294 kcal per day) (Pokempner, unpublished data). In comparison, Pontzer and Wrangham (2004) estimated that males expended slightly more energy on travel than mothers (243 versus 204 kcal per day, respectively), but this measure was calculated based on only terrestrial travel and vertical climbing and did not include travel within the canopy.

The fact that no difference in travel distance was detected may result in part from my having only sampled “central” females who tend to be more gregarious, and by definition, share a greater overlap with the male range compared to peripheral females (Williams et al. 2002b, Emery Thompson et al. 2007). Little to date is known about the behavior of peripheral females because of the difficulties inherent in their study but it appears that they use lower quality and larger core areas (Williams et al. 2002b, Emery Thompson et al. 2007, Murray et al. 2008). During this study central females spent less time alone and more time in social parties (Chapter 3) than recorded previously at this and other sites (Wrangham and Smuts 1980, Wrangham et al 1992) (Table 4.6), which may account for some similarity in male and female travel. Lehmann and Boesch (2005) suggest that the variation observed in sex differences among western and eastern populations may in part be explained by differences in use of peripheral areas by individuals rather than simply sex differences alone. Although difficult to obtain, data on these peripheral individuals will be of great importance in distinguishing whether the lack of sex differences in travel distance observed here are a byproduct of variation within females. However, while greater association between the sexes may result in similar travel patterns, the fact that males and females in this study still differed in range size indicates that this was not simply a matter of spending more time travelling together.

A comparison of sex differences in ranging among the long-term chimpanzee study sites also reveals the importance of considering the influence of demographics and territorial behavior. Male range use is expected to reflect group territoriality and in chimpanzees this is most often indicated by patrol activity. Groups composed mainly of males visit the borders of the community range in an effort to monitor their territory and, in some cases, direct incursions into neighboring territories (Watts and Mitani 2001, Watts et al. 2006). At some sites, the number of males in the community is positively associated with community range size (Lehmann and Boesch 2003 but see Gombe: Williams et al. 2004 and spider monkeys: Wallace 2007), while Williams (2000) found that, more specifically, it was the number of males in the community relative to external threats from neighboring communities that was a better predictor of range size. Since females typically do not participate in patrols (but see below), their home range is often smaller and it might be expected that communities where males patrol more frequently exhibit greater sex differences in ranging. However, despite the fact that males at both Gombe and Tai patrolled the area at the same frequency, only the Gombe community showed sex differences in ranging. This discrepancy might be an artifact of sampling protocol as Doran (1997) found sex differences in this same population, or this might reflect the fact that females at Tai are known to participate in patrols as well (Boesch and Boesch Achermann 2000). Tai also stands out among the sites as having a sex ratio heavily skewed towards females. Long-term study of ranging patterns at Tai revealed that sex differences became more apparent as community range size increased along with the number of males (Lehmann and Boesch 2004). Thus this same relation may hold across study sites and may be associated with the relative number of males. The Ngogo community is the largest known chimpanzee community (150 total individuals with 23 adult males) and is characterized by a relatively large home range (Table 4.6). Although reported values for home range and travel distance from this community are preliminary and likely to be underestimates, they nonetheless show a substantial difference between the sexes as might be predicted if demography and community range size are an important influence (Table 4.6). In addition, social and spatial subgroups are found within both males and females at this site (Mitani and Amsler 2003, Wakefield 2008). More information on sex differences within the Ngogo community will be particularly valuable in putting inter-site variation into context.

Range Use and Foraging

In general, ranging patterns in primates are primarily influenced by ecological constraints and the search for food, particularly when considering movements at the group level (Altmann 1974, Milton 1980). Although complicated by factors such as group size, foraging theory predicts that individuals will range so as to maximize foraging efficiency (Stephens and Krebs 1986). For primates who forage on resources that are patchily distributed, travel distance and range use often respond to resource availability and patch size (Terborgh 1983, Olupot et al. 1997, Ganas and Robbins 2005) and increased travel distance typically results in encountering more food resources

(Janson 1988, Norconk and Kinzey 1994). However, when viewed at the level of sex-based strategies, female ranging is expected to be more strongly linked to these patterns of foraging efficiency, whereas male ranging is often modified by behaviors related to mate and resource defense, and may thus deviate from foraging models. While both males and females in this study visited more fruit patches with greater travel, female ranging responded more to foraging parameters. Only females exhibited a response to patch size, travelling shorter distances on days when they fed in larger fruit patches. This result suggests that they were able to obtain more food in these larger patches, thus limiting the distance they had to search for subsequent food sources. This relation was not necessarily driven by party size as a previous study of this community found no association between female party size and fruit patch size (Chapter 2). However, this current study made no assessment of variation in quality of individual resources and this would need to be considered to evaluate the efficiency of patch use (Janson and Byrne 2007).

Females also exhibited a greater response to fruit availability by expanding their home range during periods when preferred fruit was scarce. This result may reflect the fact that females were also observed to spend more time feeding on fig fruits during this season in comparison to males, and thus may have used more of the range in search of these scattered resources (Chapter 2). In contrast, previous studies have shown that in periods of resource scarcity both sexes spend less time travelling (Tai: Doran 1997) and use a smaller home range (Gombe: Murray et al. 2008), females travel shorter distances (Mahale: Matsumoto-Oda 2002), and males, not females, spend less time travelling and use a smaller home range (Gombe: Wrangham 1977). On the other hand, Herbinger et al.

(2001) observed that chimpanzees in two of three communities at Tai travelled farther when food was scarce. The discrepancy between these results is most likely due to definition as many of these studies used rainfall as a proxy of season. In this study, the definition of season was based on the availability and distribution of preferred versus non-preferred fruits, according to site-specific feeding patterns. Thus while a functional difference in range use according to fruiting patterns was found, this result may not be directly comparable to previous studies and demonstrates the importance of considering the influence of fallback foods in range use.

Previous studies of chimpanzees have confirmed that females show stronger site fidelity than males, preferring smaller core areas that vary in quality, and that furthermore, this ranging pattern is related to reproductive fitness (Williams et al. 2002b, Emery Thompson et al. 2007, Murray et al. 2008). The implication of this is that females benefit from greater knowledge of the location and availability of resources within these areas as opposed to males (but see Murray et al. 2008 for seasonal male core area use). While testing the relative knowledge of the area was beyond the scope of this study, the results suggest that females may have used their range more efficiently. Females used their range in a more clumped fashion and traversed more of their total home range on a daily basis. Despite the fact that females tended to have smaller daily home ranges than males, they visited the same number of fruit patches per day, indicating that they were able to locate the same amount of resources in a smaller area. Moreover, females travelled shorter distances between all food patches and were found to travel more linearly between fruit patches, implying more directed routes between resources. However, while these findings suggest female efficiency in range use, a more accurate test must incorporate not only the resources that were visited by the individual but also the available resources that were passed along the foraging route.

While this study focused on the relation between foraging and range use using a limited number of parameters, there are alternative explanations for the observed differences not directly considered here. In many dimorphic mammals, differences in body size, or more specifically, differences in the metabolic requirements dictated by body mass, result in different ranging patterns, with larger animals tending to travel farther and using larger home ranges (McNab 1963, Milton and May 1976, Garland 1983). However, the relatively moderate level of body mass dimorphism coupled with the high energetic demands of reproduction in chimpanzees suggests that differences in body size alone may not directly correspond to differences in energetic requirements (Key and Ross 1999, Pokempner unpublished data). When costs of additional body mass in males is considered, male requirements are expected to be about 27% higher than those of females (Smith and Jungers 1997). In contrast, additional costs of reproduction would raise female requirements an estimated 25-50% above base level (Portman 1970, Oftedahl 1984, Aiello and Key 2002). Alternatively, the influence of offspring on female travel patterns may also confound sex differences in ranging since females with small infants and juveniles were found to travel shorter distances at Gombe and Kanyawara respectively (Williams et al. 2002a, Pontzer and Wrangham 2006 but see Lehmann and Boesch 2005). While sample size was limited, a preliminary investigation of this study population revealed a similar effect of infants on their mother’s DTD (Pokempner unpublished data). Perhaps more difficult to quantify is the effect of offspring on general range use – and more specifically the possibility that mothers may avoid peripheral areas due to increased vulnerability to lethal intergroup attacks and infanticide (Goodall et al. 1979, Arcadi and Wrangham 1999, Watts et al. 2006 but see Lehmann and Boesch 2005).

Overall, these results support existing models of the spatial segregation in fission-fusion species. While ultimately both males and females will benefit from ranging in a manner so as to improve foraging efficiency, males are less constrained by reproductive costs and more likely to be influenced by social factors. In a number of semi-solitary and fission-fusion species, males invest in cooperative efforts to defend resources preferred by females (cheetahs: Caro 1994; raccoons: Gerht and Fritzell 1998, kinkajous: Kays 1999). Although males are not exempt from ecological constraints and may modify their foraging behavior accordingly, particularly in times of scarcity (Murray 2006, 2008), this study shows that female range use responds more to foraging constraints. Females in this study visited the same number of patches as males but in a smaller area, expanded their home range size in relation to fruit distribution as preferred resources became scarce, and travelled more directly between fruit patches. While previous studies have suggested that females gain foraging benefits from differentiated core area use, the results of this study provide further evidence that female core area use is more related to foraging efficiency as compared to males.

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Table 4.1 Sample size and distribution among focal individuals and sexes used for determining DTD and home range size.
DTD= daily travel distance (see text for calculation).

	Focal ID	Total Focal Follow Days	Mean Length of Focal Follow	Focal Follow Days Used for DTD	Mean DTD (km)	Focal Follows Used for Home Range	Mean # GPS Points per Focal Follow	Total # GPS Points	Home Range (km^2) (98% Grid Cell)	% Time Spent Arboreal
Females	AL	14	9.6 ± 1.9	6	3.0 ± 0.9	14	30	540	6.8	70
	BL	15	9.0 ± 1.9	7	1.9 ± 1.1	15	33	433	4.5	81
	NL	13	9.5 ± 1.7	8	2.1 ± 1.1	13	36	467	5.8	78
	OU	17	9.5 ± 1.0	7	2.7 ± 0.9	17	33	535	8.5	57
	TG	15	9.2 ± 2.1	6	2.0 ± 1.1	15	27	464	5.3	78
	Mean per Individual	**15**	**9.4 ± 1.7**	**7**	**2.3 ± 0.5**	**15**	**32**	**488**	**6.2**	**73**
Males	AJ	14	9.0 ± 1.6	5	2.5 ± 0.7	14	31	438	9.5	35
	KK	15	9.7 ± 1.8	5	3.5 ± 0.9	15	31	562	10.5	44
	LK	15	8.2 ± 1.7	6	2.5 ± 1.1	15	27	412	10.3	42
	MS	14	9.6 ± 1.9	5	2.9 ± 1.7	14	32	479	9.3	34
	YB	17	9.1 ± 1.9	5	2.5 ± 0.9	17	26	520	7.8	47
	Mean per Individual	**15**	**9.1 ± 1.8**	**5**	**2.8 ± 0.5**	**15**	**29**	**482**	**9.5**	**40**

Table 4.2 GLM partial correlation coefficients for the relation between DTD and the number of fruit patches visited per day and the mean patch size of fruit trees visited per day.

	# Fruit Patches Per Day			**Mean Daily Fruit Patch Size**		
	F	partial r	p	F	partial r	p
Females	7.394	0.38	0.01	4.193	-0.53	0.05
Males	10.883	0.29	0.01	0.753	-0.46	0.40

Table 4.3 Sex differences in actual distance travelled between patches and linearity of inter-patch travel.

	All Food Patches				Fruit to Fruit Patches			
	Interpatch Distance Travelled (m)	n	Linearity	n	Interpatch Distance Travelled (m)	n	Linearity	n
Females	348.08 ± 280.56	306	0.77 ± 0.15	150	370.14 ± 290.44	140	0.80 ± 0.15	67
Males	420.27 ± 374.04	284	0.75 ± 0.14	149	443.86 ± 373.93	136	0.74 ± 0.15	68
	F=7.098, p=0.01		F=1.150, p=0.28		F=3.357, p=0.06		F=5.824, p=0.02	

Table 4.4 Sex differences in daily home range and intensity of use. Intensity is measured in terms of the proportion of the total home range that an individual covers in a day both in distance and percentage of total area.

		Intensity of Use	
	Daily Home Range (km^2)	Daily Travel Distance/Home Range ($km/\sqrt{km^2}$)	Daily Home Range/Home Range (%)
Females	0.06 ± 0.01	0.92 ± 0.14	1.00 ± 0.16
Males	0.08 ± 0.02	0.74 ± 0.14	0.81 ± 0.14
	F=4.334, p=0.07	F=5.728, p=0.04	F=4.302, p=0.07

Table 4.5 Sex differences in home range size (km^2) in response to seasonality.

	Fig Season	Non Fig Season	
Females	4.84 ± 2.06	1.99 ± 1.47	F=9.735 p=0.04
Males	8.15 ± 2.37	4.53 ± 1.99	F=3.872 p=0.12
	F=5.542 p=0.04	F=5.227 p=0.05	

Table 4.6 Comparison of male and female range use across major chimpanzee study sites.

	Daily Travel Distance (km)		Home Range (km^2)		% Time Arboreal		Patrol Rate (patrols per week)	% Time Females Spent Alone	Community Size (# all individ.s)	Community Range (km^2)	Sex Ratio (adult male: adult female)
	M	F	M	F	M	F					
Gombe	3.8	2.8	7.3	4.0	37	68	0.3	65	37	10 - 13	0.6
Kanyawara	2.4	1.9	12.1	8.5	-	-		70	50	14.9	0.7
Ngogo[1]	2.1	0.6	14.0	3.0	-	-	0.7	20	150	17.5	0.6
Tai[2]	3.7 (3.0)	3.6 (1.9)	11.3	10.5	49	65	0.3	19 (45)	35	9-13.5	0.2
Kanyawara[3] (this study)	2.8 (2.4)	2.3 (1.8)	11.7	5.9	40	73		18	55		0.7

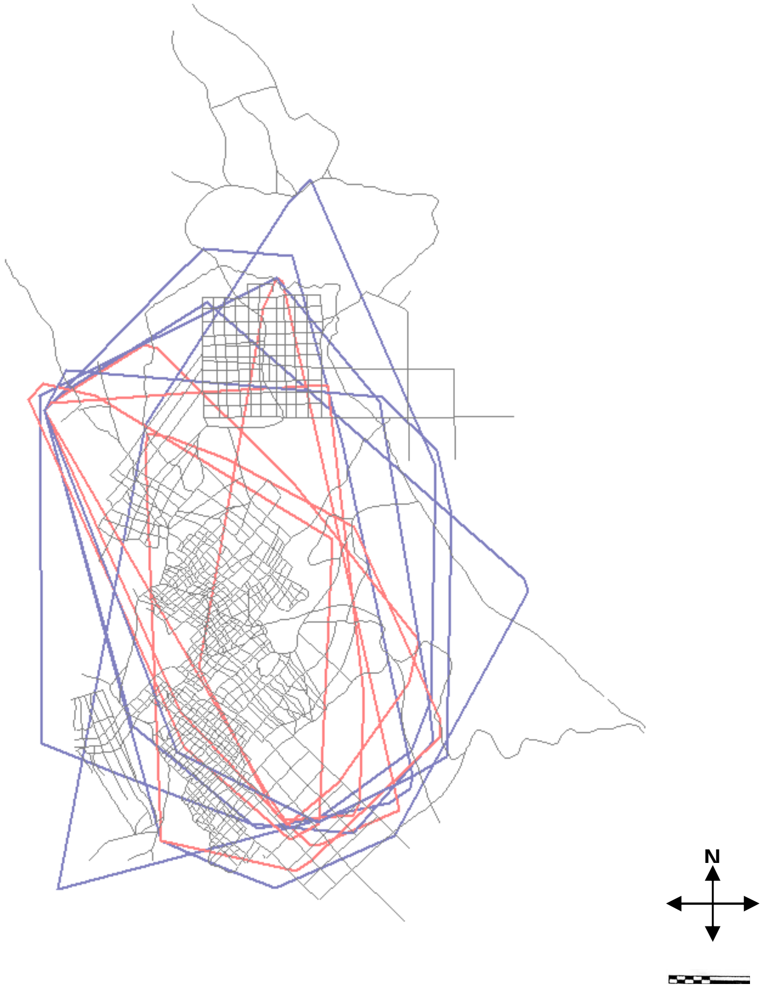
Gombe: Wrangham and Smuts 1980, Goodall 1986, Doran and Hunt 1994; Kanyawara: Wrangham et al. 1992, Chapman and Wrangham 1993, Wilson 2001, Pontzer and Wrangham 2004; Ngogo: Watts and Mitani 2001, Amsler pers. comm.; Tai: Boesch 1996, Doran 1997, Boesch and Boesch Achermann 2000, Herbinger et al. 2001

[1] Data presented on DTD and home range for each sex is considered preliminary and expected to be an underestimate for both sexes. These estimates were provided by S. Amsler and represent data collected by S. Amsler, J. Mitani and M. Wakefield.

[2] Data in parentheses from Doran 1997 using different sampling methods.

[3] Data in parentheses indicate DTD based on only terrestrial travel.

Figure 4.1 Male and female home ranges based on 98% MCP.
Home ranges of the five focal males are shown in blue and home ranges of the five focal females are shown in red. Ranges are shown in reference to the trail system which covers the extent of the known range for the Kanyawara community.



Chapter 5

Conclusion

The aim of this dissertation was to investigate the nature of sex differences in foraging in primates. By focusing on a fission-fusion species, I was able to examine 1) whether males and females differ in diet quality and foraging effort, 2) how males and females respond to variation in party size, and 3) whether differences in ranging relate to foraging. Although I dealt with each of these topics separately in the organization of this dissertation, they are highly interdependent. In this concluding chapter, I first review the major findings of this dissertation. I then synthesize these results by outlining what this study reveals about male and female strategies in a fission-fusion species. I conclude by setting these results in the context of sex differences in primates and other mammals and indicate possibilities for future research.

Dissertation Summary

In chapter 2, I examined sex differences in diet and foraging by looking more specifically at actual intake and efficiency in males and females. Sex differences were predicted due to a conflict in reproductive strategies. More specifically, females were expected to exhibit greater foraging effort in order to obtain a higher quality diet due to the energetic demands of reproduction. As males are more likely to invest in social activities related to mate competition and resource defense, it was expected that they would devote less effort to foraging. Alternatively, if male dominance over females translated into priority of access when feeding, it was predicted that they would obtain a higher quality diet. However, this study found little overall sex difference in diet quality and time devoted to foraging. Males and females were characterized by a similar absolute caloric and nutritional daily intake, although females did have a higher intake per unit body mass. Instead, males and females displayed different adaptations to variation in preferred fruit availability. Females met the challenge of reduced availability by increasing the time they spent feeding and feeding on more fig fruits. Males spent more time feeding on an herb leaf which, while of lower absolute nutritional value, had a higher energy yield due to higher ingestion rates. This difference resulted in males being more efficient foragers than females based on energetics.

While chapter 2 focused on the overall feeding strategy and intake of males and females, chapter 3 investigated how variation in party size affected these patterns. Within group scramble competition (WGS) is expected to limit optimal party size if group foraging results in a per capita decrease in intake as the number of individuals in the party increases (van Schaik and van Noordwijk 1988). This cost of WGS is often measured in terms of increased travel distance as larger groups may be forced to travel farther in order to compensate for faster rates of patch depletion (Janson and Goldsmith 1995). In chimpanzees, it is often hypothesized that females travel in smaller parties as a means to avoid the possible costs of WGS (Wrangham 2000, Williams 2002). In chapter 3, I investigated this hypothesis by comparing the effects of party size on both males and females as measured by relative intake and expenditure. I found that only females experienced greater travel costs as party size increased. However, they were able to compensate for this cost with an increase in caloric intake, but only up to a point after which expenditure outweighed intake. This critical point corresponded to the mean party size observed in the females of this study. In contrast, despite being in larger parties, males did not show any clear costs of grouping, but did reduce their party size in times of preferred fruit scarcity.

Often associated with the sex difference in gregariousness is a similar distinction in travel and range use patterns. Chimpanzee males typically travel farther and use larger home ranges than females (Wrangham and Smuts 1980, Goodall 1986, Hasegawa 1990, Chapman and Wrangham 1993, Williams et al 2002b but see Lehmann and Boesch 2005). This difference is thought to reflect the fact that male ranging should reflect mate or resource defense strategies whereas female ranging should reflect greater access to resources and more efficient and risk free foraging. In chapter 4, I attempted to relate sex differences in ranging to foraging by examining how travel distance was related to patch use and how the sexes differed in their overall range use. I did this by assuming a null foraging model which predicts that ranging will respond primarily to ecological constraints. I hypothesized that females would be more likely to fit this model if their ranging patterns reflected access to resources to a greater degree, whereas males would be more likely to deviate from this model if social factors had a greater influence on their range use. I found that while males had larger home ranges than females, both sexes actually traveled similar distances per day when all travel (arboreal and terrestrial) was considered. Females used their range in a more clumped fashion and were able to cover more of it per day. While both males and females visited more fruit patches as they travelled longer distances, female travel also varied inversely with patch size. Males and females visited the same number and same size patches on average, but females did so in a smaller area, using shorter and more linear routes.

In this study, foraging success and efficiency were measured using a variety of parameters. In some cases, these measures yielded conflicting results. This raises the question as to what is the most relevant estimate of foraging efficiency. Absolute daily energy intake was found to be similar in both males and females. While this measure provides a general proxy of meeting metabolic requirements, this only measures what is gained and does not compensate for the energy expended in the process of foraging, nor does it account for differences in metabolic costs due to reproduction. Standardizing intake per body weight may provide a more realistic measure that takes into consideration differences in male and female body mass (see Stacey 1986) and it is therefore important to note that females in this study had a higher intake of carbohydrates per unit mass. However, in this study, this measure relied on gross estimates of body mass and is therefore a general proxy that still does not reflect energy expended in the process of foraging. By incorporating energy expended while foraging (in terms of energy expended during feeding and travel between food sources), the measure of efficiency used in Chapter 2, while still based on some generalized parameters, provides a more relevant comparison in terms of fitness. In general – males and females ingested the same amount of energy, but since females expended more energy in the process of foraging (particularly due to the compounded energetic costs of reproduction) they were less efficient.

Fission-Fusion Foraging: Male and Female Strategies

Fission-fusion is rare among primates and is observed primarily in *Pan* and *Ateles* species (Goodall 1986, Symington 1987, Chapman et al. 1995). In the eastern chimpanzee subspecies (*Pan troglodytes schweinfurthii*), communities typically conform to the male-bonded model of fission-fusion (Wrangham 1979b). As large bodied, ripe fruit specialists, chimpanzees face a low level of predation (but see Boesch 1991) and a high potential for intraspecific feeding competition. With the pressures of predation reduced, the costs of permanent cohesive grouping are likely to outweigh the benefits (van Schaik 1983). This results in a system in which individuals in a community share the same home range but travel in dispersed foraging parties of varying size and composition (Kummer 1971, Wrangham 1979a, 1980, Goodall 1986). As a consequence, individuals in fission-fusion communities may have greater control over their foraging route and party membership in comparison to cohesive living individuals. Females in particular are expected to face higher costs of competition since their reproductive success depends more on access to food (Schoener 1971, Wrangham 1980). They are therefore predicted to take advantage of this flexible system and avoid competition by feeding in smaller parties and by using smaller core areas that are dispersed within the community range. Although females may benefit from being associated with a community due to pressures of between-group competition and infanticide, this model does not predict any benefits to females from social foraging. Unable to efficiently defend these dispersed females on their own, males remain in their natal group where they cooperatively defend the territory (Dunbar 1988). Males are therefore predicted to obtain benefits from grouping including defense of potential mates and the resources they depend on, increased success in cooperative hunting, and the maintenance of rank and alliances (Watts and Mitani 2002, Williams 2004, Duffy et al 2007). In general, this model has held up in the study of eastern populations with notable additions including research expanding on the nature of female-female competition (Pusey et al. 1997, Williams 2002, Murray et al. 2006), the hypothesis that lower gregariousness in mothers relates to avoidance of males (Otali and Gilchrist 2006), and evidence that males may resort to using core areas in times of resource scarcity (Murray et al. 2008).

The study presented in this dissertation also provides support for this model and is one of the first to evaluate these patterns using energetic proxies and direct comparisons between males and females. First, in accordance with the model and previous studies, females were found to be more vulnerable to the costs of grouping as indicated by increased travel and expenditure (Wrangham 2000, Williams et al 2002a). However, this study took this one step further by showing that females were largely able to compensate for high costs through increased intake and manipulation of party size. Females were thus in smaller parties than males, spending more time alone and with members of the same sex. Secondly, females travelled in smaller home ranges than males and were able to cover these areas more intensively. While this study did not look at relative quality or overlap of core area (see Kahlenberg et al. 2008), the results presented here (chapter 4) suggest that females were able to use their range more efficiently and may have benefitted from greater familiarity with the smaller range.

While models of fission-fusion focus more on the social benefits to males, this study was not able to fully test these benefits as this would require more long-term data as per Williams et al. (2004). While patrols were relatively infrequent in this community, males, unlike females, did venture to extreme areas of the known community range, suggesting that they were monitoring their territory. Results of this study however indicate that male ranging and association was not strongly affected by foraging. Unlike the results of Murray (2008), male home range and foraging behavior varied little according to fruit availability. As predicted, males travelled in larger parties and were more social. Even though larger parties did not correspond to higher travel costs in males, they did reduce their mean party size in periods of resource scarcity. Yet despite this decrease in party size, they did not alter the time they spent in social activities. However, the inverse relation found between feeding time and time spent social may indicate that social priorities constrained foraging behavior at least in terms of the activity budget. Instead, males spent more time feeding on fallback species which had a higher energetic yield per unit time as evidenced by the highly correlated relation between feeding time and energy intake.

However, some of the results presented here conflict with previous findings and assumptions of the ecological constraints model (Chapman and Chapman 2000). First, neither sex exhibited a positive relation between party size and patch size and females did not adjust their party size in response to fruit availability. In a study comparing the relationship between food availability and party size, Hashimoto et al. (2003) suggest that variation in fruit availability is less likely to affect party size when overall food abundance in the habitat is high enough to allow for “adequate” parties. Such a relationship is also reported for the Sonso community of Budongo where food is abundant and figs provide a substantial portion of the diet year round (Newton-Fisher et al, 2000). The lack of variation in female party size in this study may therefore be influenced by an overall level of high fruit availability. A preliminary comparison of the mean fruit availability during this study period with that of 12 years of data from the same site (Chapman et al. 2005) indicates that this was a relatively abundant period. This study also witnessed two peaks of the preferred high quality fruit, *Mimusops bagshawei*. As there can be high interannual variation in fruit availability at this site (Chapman et al. 1999, 2005), it is possible that males and females may vary their party size more in poorer quality years. Habitat wide indices of food availability are therefore important in understanding the plasticity of sex differences both between as well as within chimpanzee study sites.

Some aspects of female travel and association also differed from those previously recognized in studies of eastern chimpanzees. When all travel was considered, females actually travelled the same net distance as males. As discussed in chapter 4, this conflicting result may be due to the fact that females are more arboreal than males and traditional measures of daily travel distance may not fully account for this sex difference. Females also spent less time alone and more time with other females than previously reported either at Gombe or a past study at Kanyawara (Wrangham and Smuts 1980, Wrangham et al. 1992). This result was true even if the two highly associative females were excluded from the analysis. Similarly surprising was the fact that the negative effects of group size on female travel costs and feeding time were found to be primarily driven by the number of females in the group. This result may indicate that there might be a benefit to female-female grouping that justified this association. While few studies have explored this benefits argument, Williams et al. (2002) found that mothers may associate with other females in order to socialize their offspring. As more studies focus on female-female relationships, other possible benefits and social complexities are likely to emerge (Wakefield 2008). Alternatively, the discrepancy in both the travel and association results may be due to the fact that this study sampled only central females. As discussed throughout this dissertation, this sampling regime is likely to be an important factor in interpretation of these results. Since these females, by definition, had overlapping ranges, a natural consequence might be greater association among these individuals based on spatial patterns alone rather than social preference (Gilby and Wrangham 2008). However, this bias in sampling exists in most studies of chimpanzees, regardless of habituation, and these results should still be comparable. Moreover, there is perhaps a danger in lumping the behavior of peripheral and central females as this may conceal intrasexual variation.

Taken together, these results suggest that females were better able to alter party size and range use to maximize foraging relative to males. However, this idea was not necessarily supported by the nutritional and energetic data. Females adapted their foraging behavior more than males by increasing the time they spent feeding, feeding more on fig fruits, and expanding their range when preferred fruit was limited. As mentioned above, males responded to seasonality by reducing their party size and increasing the proportion of terrestrial herbs in the diet. Yet the sexes differed little in energetic and nutritional intake and males were in fact found to be more energetically efficient when preferred fruit was scarce. One possible explanation for this result (as discussed in chapter 2) is the finding that the primary fallback food of females was nutritious in terms of absolute values but lower in actual yield per minute compared to the fallback foods preferred by males. This relation was reflected in the fact that feeding time and energy intake was not positively correlated in females as it was in males. However, as cautioned in chapter 2, the measurements used in these intake calculations are general estimates and far more detailed data on feeding rates and both temporal and spatial nutritional variation is needed in order to verify that such subtle differences are not an artifact of sampling. In a similar study of orangutans, who also follow a fission-fusion pattern, Knott (1998) found that while males and females did not differ in time spent feeding, males consumed more calories due to greater inclusion of a lipid rich seed in the diet. If the major difference between males and females was the fact that males fed on items of higher yield, therefore maximizing their feeding efficiency, then this begs the question - why did females not adopt a similar strategy? As discussed in chapter 2, this may be a limitation of fully understanding the nutritional value of an item to an individual, incorporating both intake rate and digestion. Females fed more on figs which are an important source of metabolizable energy as well as calcium (Conklin and Wrangham 1994, O'Brien et al. 1998). However, they are also high in water content and this may complicate actual intake yield. Alternatively, this distinction may be influenced by general behavior. It is important to note that the herb leaf favored by males occurs in large open fields, often growing on the site of recently abandoned logging camps and near paths in the forest (pers. obs.). While there is little to no threat of natural predation, these areas are often exposed and frequented by humans and may be perceived as dangerous by mothers, particularly when alone or in small parties. This potential vulnerability coupled with the arboreal nature of females may explain why they did not spend as much time feeding on this herb as males did. Given that logging recently ceased in Kibale National Park, new and large patches have quickly grown up throughout the community range. The importance of this fallback food in the diet may therefore be a relatively recent and perhaps temporary development. Long term analysis of changes in the composition of the diet of the community will reveal the significance.

While males and females had a similar overall activity budget and intake, males were found to be more efficient foragers in terms of net energy intake. Apart from the difference in food selection discussed above, this contradictory result most likely reflects the additional energetic costs that reproduction imposes on females. Based on difference in body mass alone, chimpanzee males would be expected to incur costs nearly 27% higher than those of females. However, when the costs of reproduction are factored in, energetic expenditure for females is increased on average 38% over their reproductive cycle (25% during gestation, 50% during lactation). Since males and females in this study were found to spend the same time feeding and travelling, covered the same daily distance, and consumed a similar amount of calories overall, this implies that the key determinant of relative efficiency was the added cost of reproduction factored into the energetic expenditure calculations. Although not included in the results presented in this dissertation, an additional analysis revealed that estimates of daily energetic expenditure were in fact about 15% higher for females than males (Pokempner unpublished data).

The fact that females were found to be less efficient suggests that females did not necessarily compensate for added reproductive costs with greater intake, as might be expected. While sample size was too small for an adequate test, a preliminary comparison of intraindividual variation among the females in this study did not reveal any significant differences in diet, intake or foraging behavior according to reproductive phase

(Pokempner unpublished data). Such a lack of a clear patterns was also found in an analysis of the long-term feeding behavior of females at Gombe (Pandolfi 2005). One notable exception in the current study, however, was the one focal female who conceived during the study period. Consistent with Knott's "ecological energetics" hypothesis, which suggests that chimpanzee ovarian function is mitigated by energetic balance and intake (Knott 2001, Sherry 2003, Emery Thompson 2005), this female exhibited a particularly low amount of variation in energy balance over the course of the study and showed a dramatic peak in energy intake during the period of conception which coincided with fruit abundance (Pokempner, unpublished data). While only anecdotal, this evidence supports previous research, based on both behavioral and hormonal observations, that females respond to acute changes in resource quality and are more likely to conceive during periods of high availability, particularly in habitats with unpredictable patterns of resource availability (van Schaik and van Noordwijk, 1985, Koenig et al. 1997, Emery Thompson 2005). This hypothesis also predicts that seasonal adaptation and choice of fallback foods are particularly important to reproductive females (Knott 2005). While more precise data is needed to evaluate the importance of specific food items during reproduction in the study population, it is nonetheless notable that the key difference between males and females in this study was the choice of fallback foods. In addition, females were found to consume more calories per unit body weight which may be a more biologically appropriate measure relative to males. Knott (2001) suggested that less extreme seasonality and the availability of higher quality fallback foods would result in less variation in chimpanzee energy balance as compared to orangutans who experienced more extreme mast fruiting seasons. In a population of

Sumatran orangutans characterized by a more chimpanzee-like pattern of fruit availability, fluctuating between preferred and fig fruit, Wich et al. (2006) found that individuals did not experience a negative energy balance as measured by trace ketones in the urine. Although ketones have not been successfully recorded in wild chimpanzees (Emery Thompson, pers. com.), measuring levels of a metabolite of insulin (C-peptide) may provide a comparable method to more accurately gauge energetic status and may better evaluate whether a female reliance on more fig fruit during the scarce season had an energetic impact (Sherry and Ellison 2007).

In summary, Wrangham (1986, p. 365) effectively stated the classic view of chimpanzee socioecology as follows (italics added by A. Pokempner):

> "If the competition hypothesis is correct, *party foraging reduces feeding efficiency significantly*. This means that the best strategy for females, *whose reproduction is presumed to be limited by food intake*, is to *spend most of their time alone*. On the other hand, *party foraging allows sufficient feeding time* that males, whose *reproductive interests depend critically on male bonds*, are able to *spend much of their time in parties*."

While this pattern has been supported in a number of studies of chimpanzees, some of its components (in italics) have only recently been tested at a more detailed level involving energetics, intake and reproductive success. Recent studies of long term data have now provided evidence that intake and male bonds are indeed closely linked to female and male reproductive success respectively (Watts and Mitani 2001, Emery Thompson 2005, Duffy et al. 2007). In this study I showed that party foraging reduced feeding efficiency, but only for females, and only on the occasions when they were in particularly large parties (larger than their mean party size). However, females in this study did not spend most of their time alone. Although males did not increase feeding time in response to resource fluctuation, they were able to spend much of their time social and in larger parties and were still able to obtain a high quality diet.

An Ecological Battle of the Sexes?

According to reproductive theory, females are expected to maximize their energy intake in order to sustain the high costs of reproduction whereas males are more likely to invest energy in the pursuit and defense of available mates (Schoener 1971). This inherent reproductive conflict is therefore expected to translate into differences in foraging. However, among primates, there is little evidence of a consistent pattern of sex differences. This lack of consistency is in part due to the fact that factors typically influencing these differences, such as mating system, sexual dimorphism, dominance regime, and diet vary greatly among primate species. Most studies which address sex differences reveal that overall, females often spend more time feeding than males (capuchins: Fragaszy 1986, 1990, van Schaik and van Noordwijk 1989; red colobus: Marsh 1981; mangabeys: Waser 1977; orangutans: Mitani 1989). Females may also increase the rate at which they feed, relative to males, as has been observed in the titi monkey (Kinzey 1977) as well as the monomorphic siamang (Chivers 1977). Often these differences are largely confined to specific phases of reproduction, with females increasing time spent feeding (mountain gorillas: Watts 1998; baboons: Altmann 1980, Silk 1986, Stacey 1986, Muruthi et al. 1991, Dunbar and Dunbar 1988; howler monkeys: Smith 1977; sifaka: Saito 1998; ring tailed lemurs: Sauther 1994), increasing the amount of protein in their diet (guenons: Gautier-Hion 1980, Cords 1986; capuchins: Robinson, 1981, Fragaszy 1986; red colobus: Clutton-Brock 1977; squirrel monkeys: Boinski 1988; muriqui: Strier 1991) or decreasing travel (baboons: Altmann 1980) primarily during the particularly demanding phases of pregnancy and lactation. In other cases, it is males that may spend more time feeding than females, as has been observed in green monkeys (Harrison 1983) and the highly dimorphic mountain gorilla (Watts 1998). However few of these studies consider seasonal variation or relative energetics and nutrition (but see Knott 1998, Nakagawa 2000). As this dissertation illustrates, what appears as overall similarities in behavior may mask divergent seasonal adaptations as well as differential nutritional intake.

At the other extreme, more work has focused on sex differences in sexually segregated species, particularly large bodied herbivores (Du Toit 2005). These species are typically characterized by high levels of sexual dimorphism and clear seasonal breeding periods during which the sexes converge (Mysterud 2000). Sexual segregation is often discussed in terms of either social or habitat segregation, although the two are interrelated (Conradt 2005). A variety of hypotheses have been put forward to explain this phenomenon in ungulates and range from the influence of activity budgets to sex differences in predation risk (see Ruckstuhl and Neuhaus 2000 for review). However, while few of these are directly applicable to primates due to different social and ecological constraints, the “social preferences hypothesis” may be particularly relevant to the study of sex differences in chimpanzees and other species with male philopatry (Watts 2005). According to this hypothesis, males form social bonds and preferentially associate from a young age, in part as a way to develop improved mate competition skills, thus resulting in a social segregation of the sexes that could also lead to habitat segregation and differences in activity synchrony (Bon and Campan 1996, Ruckstuhl and Neuhaus 2000). Boesch and Boesch (1984) and Pandolfi et al. (2003) found that this hypothesis best explained the commonly cited sex difference in meat eating and termite fishing in chimpanzees. Pandolfi (2005) extended this hypothesis to sex differences in general feeding behavior at Gombe, and cited the fact that males overlapped more in diet, had a narrower diet than females, and spent more time feeding in larger fruit patches as evidence to support this logic. While I found no difference in the size of fruit patches used by males and females, males did spend more time feeding on TPL, which often occurs in super-abundant, non contestable patches (pers. obs.). As discussed in chapter 3, there was no relation between time spent feeding on TPL and party size in males nor was there a significant relation between time spent social and TPL feeding (Pokempner unpublished data). However, when considered in relation to females, who consistently travelled in smaller parties and fed less on TPL, this might indicate that this dietary choice sustained larger parties as related to females (but see above for discussion of influence of arboreality and nutrition as well).

Future Directions

While this research expanded the study of sex differences, its limitations also exposed areas for future study. In particular, more data is needed on the influence of both intra-sex and intra-individual variation in feeding and intake. As previously discussed, it is likely that peripheral and central females differ in their foraging strategy since they are known to vary in reproductive fitness (Pusey et al. 1997, Williams et al. 2002b, Emery

Thompson et al 2007). In general, recent research suggests that inter-female relations may be more complex than previously thought and that dominance and coalitions may play a greater role in their foraging behavior (Wittig and Boesch 2003, Wakefield 2008). Similarly, since male hierarchies are clear and regularly reinforced through aggression, males may be expected to differ in relative intake according to dominance rank, but there is little evidence to support this hypothesis as of yet (but see Watts and Mitani 2002 for relation between male relations and meat sharing).

In addition, it is unrealistic to expect that sex based strategies act independent of each other. It is therefore necessary to consider the impact of males on females and vice versa. For instance, this study did not factor in the effect of estrous females on the foraging behavior of either sex. The presence of estrous females typically results in the formation of larger parties for both males and anestrous females (Mitani et al. 2002) and will therefore introduce a confounding influence on observable sex differences. In theory, it is expected that male mate competition will escalate during periods of female receptivity and that this might result in males devoting more energy to competition and mate guarding at the cost of foraging as has been observed in other primates (Packer, 1977, Alberts et al., 1996, Nakagawa, 2000). Although anecdotal, it is of note that the focal male in this study who was observed to challenge the alpha male also experienced the lowest energy balance (low intake relative to expenditure) on a day in which he and the alpha were competing over an estrous female. Future research will address this question by comparing the energetic investment in status and mating competition by males of different rank at Kanyawara (Georgiev, pers comm). Similarly, as suggested in chapter 2, males may exert an indirect influence on female foraging behavior and this is currently the topic of research in the Budongo community (Machanda, pers. comm.). While there is little evidence of males outcompeting females for food resources through direct aggression, it is possible that females actively avoid males. Such a strategy seems to be common in other fission-fusion species (grizzly bear: Wieglus and Bunnell, 1994, dolphins: Martin and da Silva 2004). However this aspect is particularly difficult to measure and will require a more sophisticated study design.

Overall, the results of this study suggest that female range use may be more related to foraging efficiency than males and this is likely to reflect difference in knowledge of their home range. However much more targeted studies are needed to test the relative spatial abilities of males and females. Gaulin and Fitzgerald (1986, 1989) hypothesized that sexual selection in polygymous mammals results in sex differences in spatial abilities such as navigation. Males, driven by mate competition, are expected to benefit from navigational skills in long range travel, and in cases of species utilizing weapons (e.g. humans, chimpanzees), the ability to use projectiles. Females are hypothesized to employ a low risk strategy focusing on resource acquisition and are therefore expected to benefit from memory skills (Gaulin and Fitzgerald 1986, 1989, Ecuyer-Dab and Robert 2004a) These factors are in turn expected to be related to sex differences in range size (Jones et al. 2003, Ecuyer-Dab and Robert 2004b). A number of studies ranging from rodents to humans support this idea, indicating that males excel in tasks related to spatial navigation and projectile manipulation whereas females have a superior spatial memory and rely more on landmarks (Williams and Meck 1991, Silverman and Eals 1992, Sandstrom et al. 1998, Barkley and Jacobs 2007). Such a distinction in humans may be further related to the development of the division of labor in hunter gatherer societies (McBurney et al. 1997). This observation is particularly relevant as chimpanzees are also observed to engage in both hunting and the use of weapons (Goodall 1986, Wrangham and Peterson 1996, Pruetz and Bertolani 2007). While captive studies have tested the cognitive abilities of chimpanzees, few have done so in the wild, particularly in reference to sex differences (Menzel 1974, Boesch and Boesch Achermann 2000). Future research using more sophisticated tests of cognitive foraging ability (c.f. Janmaat et al. 2006, DiFiore and Suarez 2007, Janson and Byrne 2007) in wild male and female chimpanzees are needed to better understand the role of sex differences in the evolution of more advanced cognitive foraging skills.

In conclusion, this study provides evidence to support long-held hypotheses regarding the nature of sex differences in fission-fusion species. Specifically, females are more susceptible to resource competition in larger parties than males and use their range more in response to resource use. Despite these differences, males and females exhibited similar overall foraging effort and nutritional intake. This similarity masked important differences including a distinction in the reliance on fallback foods as well as seasonal changes in activity budgets and party size.

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