ABSTRACT

BEAVER, LILYANNE CAITLYN. Foraging Metrics Affected by Reproductive and Residential Status in Young Female Eastern Chimpanzees (*Pan troglodytes schweinfurthii*) (Under the direction of Dr. Kara Walker and Dr. Christopher Walker).

In chimpanzees, most females disperse from their natal community upon the onset of sexual maturity, while some remain and begin reproducing in their natal group. In this study, I examine the impact of residential and reproductive status on female chimpanzee diet composition and quality using long-term foraging data from young sexually mature female chimpanzees in Gombe National Park. Female chimpanzees were classified into three groups based on residential status and reproductive stage: sexually mature natal, sexually mature immigrant, and primiparous pregnant. Diet quality was assessed holistically using diet breadth, percentages of fruit, leaves and pith, meat, insects, and preferred foods in the diets of female chimpanzees after sexual maturity and through first pregnancy. I found female status to be a significant predictor of the amount of time a female spends foraging ($p=0.03$), with primiparous pregnant females and sexually mature natals feeding for longer than sexually mature immigrants. Female status did not significantly predict any other foraging metric. When analyzing solely primiparous pregnant females, residential status did predict differences in meat consumption, with immigrants eating nearly significantly more meat during their first pregnancy ($p=0.05$). Residential status did not affect any other foraging metric during first pregnancy. These results suggest that diet composition in female chimpanzees only marginally differs due to residential or reproductive status, likely due to integration tactics utilized by incoming immigrants to avoid food scarcity after permanent dispersal. Any dietary changes that did occur between sexual maturity and first pregnancy occurred exclusively in immigrants, with immigrants increasing their time spent foraging and possibly their meat consumption upon first pregnancy.

Foraging Metrics Affected by Reproductive and Residential Status in Young Female Eastern Chimpanzees (*Pan troglodytes schweinfurthii*)

by
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A thesis submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Master of Science

Biology

Raleigh, North Carolina
2023

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BIOGRAPHY

Lilyanne Beaver was born on May 6th, 1999, in Jacksonville, Florida to Michael and Susan Beaver as the eldest of six. Growing up in the ecologically diverse state of Florida, she found herself interested in the biological sciences from a young age through fascination with fossils, bones, and animals. As an undergraduate student at Florida State University, she was able to realize these interests through the discovery of physical anthropology and evolutionary biology. While pursuing her Bachelor of Science in Anthropology and Biological Sciences, she worked in the Anthropology department's osteology laboratory and performed field biology work investigating the function of biofluorescence in tree frogs. Given her interest in human evolution, ecology, and animal behavior, Lilyanne was naturally drawn to the study of primates. This was solidified through her part-time work as a tour guide and primate husbandry intern at the North Florida Wildlife Conservation Center, where she had the opportunity to work directly with ring-tailed and ruffed lemurs. Shortly after her graduation as the first in her family in April of 2021, she moved to North Carolina to begin her graduate studies in primatology at North Carolina State University. Upon graduation, Lilyanne plans to pursue an academic career in evolutionary anthropology.

ACKNOWLEDGMENTS

I would first like to thank my advisor, Dr. Kara Walker, for her willingness to supervise my project based on her years of hard work and data collection on the female chimpanzees of Gombe. I am extremely grateful for all the time, advice, and guidance you have given me.

I would also like to thank Dr. Christopher Walker for allowing me the opportunity to pursue this degree and for welcoming me into the lab.

I would like to thank my additional committee members for each of their help with my research and other contributions to my time here at NC State. Thank you to Dr. Lisa Paciulli, who provided me with guidance and opportunities to refine and expand upon my teaching skills. Thank you to Dr. Ann Ross, who very kindly welcomed me into her lab and allowed me to pursue my interest in forensic anthropology.

I would also like to thank all my family and friends who have supported me through my academic career.

A special thank you to Abigail, for supporting me endlessly through graduate school applications, the move to North Carolina, and the program itself. I could not have done it without you.

And thank you to the young female chimpanzees at Gombe, I hope to thank you in person one day!

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INTRODUCTION

Access to energy directly limits reproductive timing and success in mammals (Trivers, 1972). Reproduction is energetically and nutritionally costly for female mammals, lactation especially so (Speakman, 2007). To mitigate the energetic requirements of gestation and lactation, female mammals often adapt behaviorally to increase their caloric intake by foraging more frequently and focusing their efforts on high-quality foods (Lee, 1987; Gittleman and Thompson, 1988). Compared to other mammals, primates exhibit extended periods of lactation and gestation and slower postnatal growth than expected for their body size (Dufour and Sauther, 2002). This helps spread out the costs of reproduction over a longer period, meaning that female primates have more flexibility in adapting to meet daily energetic requirements during reproduction than other mammals their size.

Despite many primate species specializing in certain foods, such as fruits or leaves, their ability to flexibly adapt their feeding behavior allows them to cope with the seasonal variations in food availability (Lambert and Rothman, 2015). Many primate species are classified as frugivores or folivores, and all of them can accommodate seasonal availability of preferred foods. Chimpanzees (*Pan troglodytes*) are flexible omnivores (Goodall, 1986) and a main staple in their diet is ripe, fleshy fruits (Wrangham et al., 1998). Access to energy in the form of food is crucial to reproductive success in these primates. Captive populations of chimpanzees that receive adequate nutrition show accelerated reproductive schedules compared to wild ones (Emery Thompson, 2013). Similarly, females in provisioned wild populations like Gombe and Bossou had shorter observed interbirth intervals compared to females in non-provisioned sites (Nishida et al. 2003). In many natural habitats, the fruit preferred by chimpanzees is often patchy and seasonally unpredictable (Wrangham and White, 1988), resulting in periods of food scarcity.

When food is scarce, switching to fallback foods to mitigate energetic disparities is one behavioral adaptation primates utilize (Hemingway and Bynum, 2005). Fallback foods are generally considered more inefficient options as they are typically lower in nutrients and take more energy to digest (Wrangham et al., 1991), so a diet high in fallback foods is indicative of poor diet quality. To maximize foraging efficiency in periods of resource scarcity, chimpanzees are known to modify their grouping patterns by decreasing the size of their foraging parties (Matsumoto-Oda et al., 1998).

The reproductive state of a female chimpanzee impacts her foraging and grouping patterns based on energetic requirements and competition. In many populations, females spend more time traveling and foraging alone or with dependent offspring in a restricted area of the larger range than males who travel primarily in groups throughout the wider community range (Wrangham and Smuts, 1980). Females typically have high site fidelity to their core areas, which makes foraging efficient (Murray et al., 2007). Once they are sexually receptive, females more frequently travel away from their mother's core areas and join larger foraging and hunting parties (Goodall, 1986). This puts females in closer proximity to males and to the scramble competition for fruit associated with group foraging (Wrangham, 2000). When pregnant and lactating, females then return to more solitary foraging patterns (Wrangham and Smuts, 1980), and focus their foraging effort on high-quality foods (Murray et al., 2009).

Additionally, chimpanzees are unusual among primates in that upon sexual maturity, females rather than males disperse and immigrate into new communities (Pusey, 1980). This presents unique challenges to young female chimpanzees immigrating into their new communities. New immigrants may experience issues obtaining high quality fruits due to female aggression (Pusey, 1980), low dominance rank (Murray et al., 2006; Foerster et al., 2016),

unfamiliarity with the novel environment (Piper 2011), or loss of kin support (Goodall 1986; Walker and Pusey, 2020). This time following dispersal is especially sensitive for reproductive rates because dispersal occurs around the onset of sexual maturity and can delay timing of first birth by 2.5 years on average (Walker et al., 2018). Thus, working to minimize dispersal costs and reduce the integration period may be a high priority for young dispersing females. Understanding the factors that influence female chimpanzee use of high-energy, preferred foods, and thus diet quality, in this time following dispersal will offer vital insight into chimpanzee reproductive and behavioral ecology.

1. Chimpanzee Group Structure

Social group structure impacts the way individuals interact with their environment and can offer insight into how competition for resources is mitigated. Wild chimpanzee populations use a fission-fusion community structure that consists of permanent social groups with "parties" that split and merge over time as animals move through their environment (Aureli et al., 2008). These parties are highly fluid and can vary in sex composition and number of individuals based on food availability, sexual receptivity of females, and predation risk (Nishida, 1968; Goodall, 1986; Wrangham, 2000). Male chimpanzees are characterized as being highly gregarious and typically form social bonds with other males. Males work together to patrol and defend the territory of the larger permanent social group, and this protects both the food resources and resident females from outgroup males (Nishida, 1968; Wilson and Wrangham, 2003; Williams et al., 2004). Although males within a permanent group may create cliques based on rank and age, they maintain community integrity and do not show much aggression between subgroups (Mitani and Amsler, 2003).

In contrast, females are considered less gregarious and more solitary, typically spending more time alone and traveling in smaller parties than males (Goodall, 1986; Wrangham, 2000). In the scramble competition hypothesis, Wrangham (2000) posits that the higher travel costs associated with transporting infants incurred by female chimpanzees makes it more efficient for them to forage solitarily in a single core area, rather than scrambling for high-quality food patches dispersed throughout the community range. For example, wild female chimpanzees are commonly observed as having high fidelity to small core areas that overlap with other females in clusters and usually forage alone or with their offspring (in Gombe: Goodall, 1986; Williams et al., 2002; in Kanyawara: Emery Thompson et al., 2007).

However, gregariousness and the degree to which females restrict their ranging varies between populations and depends on community size, resource availability and other factors (Williams et al., 2004). In the chimpanzee population at Tai Forest in Côte d'Ivoire, females had similar levels of home range usage (Lehmann and Boesch, 2005) and levels of sociality (Lehmann and Boesch, 2008) as males. Females in the large Ngogo community of Uganda are also relatively gregarious and choose to spend most of their time with other females in cliques (Wakefield, 2008; Wakefield, 2013). It is likely that a greater abundance of food in these communities allows for females to be more gregarious when compared to smaller sites like Gombe and Kanyawara (Wittiger and Boesch, 2013).

2. Dispersal and Reproduction

Natal dispersal, a tactic in which individuals of one sex relocate from their birth community into another for reproduction, is common in primates and other social mammals (Pusey and Packer, 1987). In most social mammal species, females remain in their natal groups

and receive the benefits of social support and kin cooperation, which increases reproductive success (Silk et al., 2003). In these species, males disperse in search of mating opportunities outside of their natal communities (Jack and Fedigan, 2004). Chimpanzees are unusual in that males are the philopatric sex, so females disperse from their natal groups during adolescence (Pusey, 1980). Female primates invest heavily in reproduction compared to males (Trivers, 1972), creating a precarious situation for female chimpanzees who must balance the costs of dispersal and reproduction.

Female chimpanzees typically disperse within two years of reaching sexual maturity, which occurs around age 11 and coincides with the onset of anogenital swellings (Emery Thompson, 2013; Walker et al., 2018). Female chimpanzee natal dispersal rates can vary between communities, though most communities experience high levels of female dispersal at around 90% (Pusey and Schroepfer-Walker, 2013). However, in the Kasekela community at Gombe National Park, only 50% of the female chimpanzees disperse, while 83% of the females in the neighboring Mitumba community disperse (Pusey et al., 1997; Walker et al., 2017). It has been suggested that Kasekela's low dispersal percentages may be due to historical provisioning at the field site or population declines in neighboring communities (Walker and Pusey, 2020). Regardless, this phenomenon that results in both immigrant and natal adult females within the Kasekela community makes it an indispensable study site for observing the causes and effects of natal dispersal in female wild eastern chimpanzees (*Pan troglodytes schweinfurthii*).

There are a few factors that influence a female's decision to stay in her natal community or disperse to another. Some researchers have proposed inbreeding avoidance to be the main driver of natal female dispersal (Pusey, 1980; Clutton-Brock, 1989). Mating between related individuals can lead to inbreeding depression and an increase in recessive deleterious alleles,

which results in diminished survivability and fertility of offspring (Charlesworth and Willis, 2009). A recent study of Gombe chimpanzees found that the presence of maternal brothers increased female's likelihood to disperse from their natal group (Walker and Pusey, 2020). This was true even when controlling for alternative factors like resource availability and intrasexual competition, pointing to inbreeding avoidance as an important significant factor influencing female dispersal in chimpanzees (Walker and Pusey, 2020).

However, there has been disagreement concerning the role of inbreeding avoidance in the likelihood for a natal female to disperse (Moore and Ali, 1984), with some researchers finding that it is not a significant driver in chimpanzee populations (Stumpf et al., 2009). Instead, alternate factors have been suggested to drive female dispersal in chimpanzees, such as intrasexual competition for mates and resources (Pusey and Packer, 1987). Resource availability is known to influence dispersal patterns in chimpanzees, as females in Kanyawara wait to disperse for favorable foraging and energetic conditions to arise (Stumpf et al., 2009).

In addition, female natal dispersal is influenced by maternal presence in Gombe, especially when the mother is high-ranking (Walker and Pusey, 2020). Walker and Pusey (2020) found that females with high-ranking mothers were more likely to stay in their natal groups compared to orphans or daughters with low-ranking mothers. These maternal relationships can help females procure food from high-quality patches throughout adulthood, since mothers frequently share foraging areas with their adult daughters (Goodall, 1986). Thus, the strength of a maternal relationship may be an especially important consideration for females when deciding to disperse and, in certain circumstances, may outweigh the risks of possible inbreeding.

Dispersal can be divided into three stages: emigration from the old community, movement throughout the interpatch matrix, and immigration into the new community (Bowler

and Benton, 2005), and each of these stages incurs unique costs for the dispersing animal (Bonte et al., 2012). For example, dispersing roe deer expended 22% more energy than their

ic counterparts during the transience stage of dispersal (Benoit et al., 2019). At Kanyawara, availability of ripe fruit is associated with earlier dispersal times, meaning that female chimpanzees may wait to disperse until they have sufficient energy reserves (Stumpf et al., 2009). These energy reserves could be used to offset the energetic costs associated with traveling to new communities. However, little is known about exactly what those travel costs are for chimpanzees. Traveling shorter distances by dispersing to adjacent communities is common between Mahale and Gombe populations and may help mitigate travel costs (in Mahale: Nishida, 1979; in Gombe: Walker, 2015). However, female chimpanzees have also been observed dispersing longer distances, such as when habitats are fragmented and there are no adjacent communities present (McCarthy et al., 2018). This would likely result in higher travel costs.

Although aggression between female chimpanzees is not as common as it is between males (Goodall, 1986), competition for resources can lead to social repercussions of dispersal, such as aggression toward immigrants from resident females (Pusey, 1980). Female aggression toward immigrants is a significant driver in female-female aggression in every studied chimpanzee site (at Mahale: Nishida, 1979; at Tai: Boesch and Boesch-Achermann, 2000; at Kibale: Kahlenberg et al. 2008b; at Gombe: Pusey et al., 2008). In Kanyawara, aggressive encounters increase four-fold when new immigrant females are present in the community than when there are not (Kahlenberg et al., 2008b). Moreover, cases of infanticide by resident females against newborns of immigrants have been reported in Budongo (Townsend et al., 2007), likely due to competition pressures. Moreover, lack of kin can also harm an individual's chance of

creating social bonds in the new community, as female chimpanzees prefer to associate with kin over non-kin (Foerster et al., 2015).

Aggression from resident females can result in stress-related and reproductive repercussions for immigrant females. In the Kanyawara community, immigrant females had higher urinary cortisol levels than natal females, likely because of aggressive encounters (Kahlenberg et al., 2008a). These costs can also affect the timing of reproductive events. For example, in the Kasekela community where only 50% of the females disperse, the age at first birth for natal females is on average about two years earlier than it is for dispersing females (Walker et al., 2018). Aggression from resident females against immigrants is likely associated with competition over foraging space, especially the important core feeding areas that female chimpanzees prioritize. Overall, the energetic and social costs associated with dispersal affect female chimpanzees' diet quality and thus reproductive health.

3. Chimpanzee Diet

Chimpanzees primarily prefer to feed on ripe fruits and specific dietary patterns are unique to each community based on local availability of resources and group culture (McGrew, 1983; Nishida et al., 1983). The ripe flesh of fruit is a high-quality food source, as it provides readily available energy. When possible, chimpanzees exclusively feed on ripe fruits (Wrangham et al., 1998). However, many of the fruit species that make up a large portion of the chimpanzee diet are seasonal, which can cause competition over fruit patches and food scarcity in the off-season (Conklin-Brittain et al., 1998; Wrangham, 2000; Wessling et al., 2018). Chimpanzees are known to have lower body masses in the dry season compared to the wet season, which may be caused by the decreased availability of preferred fruits at the end of the wet season (Pusey et al.,

2005). When fruit is not available, chimpanzees often rely on different non-fruit plant parts as fallback foods such as pith, leaves, and stems (in Kibale: Wrangham et al., 1998; at Ngogo: Watts et al., 2011). These fallback foods are generally considered more inefficient options, as they are typically lower in nutrients and harder to digest (Wrangham et al., 1991; Watts et al., 2011). Higher amounts of leaf and pith consumption has been found to negatively correlate with body mass in chimpanzees (Gilby et al., 2006), further solidifying these food choices as indicators of poor diet quality. Thus, literature on chimpanzee foraging behavior typically regards a diet that is high in ripe fruit consumption and low in overall breadth as high-quality, while a lower quality diet may contain more fallback foods and be wider in breadth.

3.1 Faunivory

Compared to the fruit and other plant matter that dominates chimpanzees' diets, carnivory plays a much smaller role in the overall composition of the food budget (Goodall, 1986). However, predation upon other vertebrates by chimpanzees is well-documented, as males engage in group hunts for red colobus monkeys (*Colobus badius*). Red colobus are the most targeted species for group hunts (Mitani and Watts, 2001; Gilby et al., 2017), and chimpanzees hunt them at every site where the two species coexist (Uehara, 1997). Hunts can be lengthy, lively, and energetically expensive, as colobus monkeys are arboreal. Thus, participating in group hunts can incur many costs for the participants, such as considerable energy expenditure (Ponzter and Wrangham, 2004), and risk of injury (Boesch and Boesch, 1989). Success in red colobus hunting is also impacted by the size of the hunting party. In some communities, hunting success increases as party size increases (at Tai: Boesch, 1994; at Ngogo: Watts and Mitani, 2000). However, chimpanzees at Gombe suffer a loss of meat per capita when hunting party numbers increase

(Gilby et al., 2006), and hunting success is high for solitary hunters in this community (Boesch, 1994). This further complicates the role of carnivory amongst chimpanzees.

The meat scrap hypothesis provides an explanation for why group hunting among chimpanzees persists despite these factors, positing that small amounts of meat are sufficient to provide chimpanzees with the nutrients necessary to balance the costs of group hunting (Gilby et al., 2008; Tennie et al., 2009). Animal source foods can provide chimpanzees with trace nutrients such as iron, zinc, and B12 that are not found readily in plant source food (Milton, 2003; Tennie et al., 2009). Thus, group hunting and meat eating may be driven more by nutritional needs, which may be met by just meat scraps, rather than caloric needs. These nutrients that meat provides may also be vital to pregnant females, as nutrient deficiencies can lead to reproductive consequences in humans (Gernand et al., 2016).

The social influences of meat-sharing in chimpanzees have been greatly debated. Females sometimes participate in group hunts for monkeys but catch less animal prey overall compared to males (Gilby et al., 2017). Thus, male chimpanzees are responsible for most of the captures of animal prey, and as a result are often given the opportunity to share meat with females. The meat-for-sex hypothesis has attempted to explain the social behavior of meat-sharing by male chimpanzees with females, proposing that meat is often exchanged for sexual access (Stanford et al., 1994). This theory has been supported by data from the Tai community, which suggests that sexually receptive females traded sex for meat, but only over long periods of time (Gomes and Boesch, 2009). Other researchers have negated the meat-for-sex hypothesis in short-term time frames (Mitani and Watts, 2001; Gilby, 2006), and have ultimately found that male chimpanzees do not prefer to share meat with sexually receptive females (Gilby et al., 2010). Gilby has found evidence for an alternative hypothesis that meat-sharing occurs to avoid having to defend a food

source from male and female beggars (Gilby, 2006). This hypothesis is strengthened further if group hunting is truly driven by nutritional benefits instead of caloric benefits, as maintaining possession of the entire kill may not be worth the costs of harassment from others.

Although the social influences of meat-sharing have yet to be fully clarified, female access to meat and the nutritional benefits that accompany it varies depending on reproductive state and dominance (O'Malley et al., 2016). Interestingly, O'Malley (2016) found that pregnant females consumed more meat than nonpregnant females and that low-ranking females were responsible for this increase. In other words, high-ranking females' meat consumption between reproductive states did not vary, but low-ranking females' did (O'Malley et al., 2016). This points to the possible influence of dominance rank and reproductive state on access to meat shared by males. This may be influenced both by social factors, such as male preference for certain females, and physiological needs, such as female motivation for nutritional supplementation during pregnancy.

Insectivory is another form of faunivory that can supplement chimpanzees' fruit-heavy diet. Insects provide a key source of nutrients, fat, and protein (O'Malley and Power, 2014). The Kasekela chimpanzees prefer to eat social insects that have similar levels of energy, fat and protein per gram to meat sourced from vertebrates (O'Malley and Power, 2012). These insects, such as ants and termites, are also typically available in highly concentrated areas, and tool technology may be employed to gather insects more efficiently (McGrew, 1992). While the nutritional benefits provided by insectivory may be helpful during gestation, the relationship between chimpanzee pregnancy and consumption of insects has not been extensively studied. One study that did analyze insectivory in pregnant female chimpanzees found that there were no

differences in insect consumption by females in different reproductive states or dominance ranks (O'Malley et al., 2016).

Chimpanzees also display sex-based variability in hunting and meat-eating. Though meat is a small percentage in the diets of both sexes, male chimpanzees are more commonly observed hunting animal prey, especially the red colobus mentioned previously. Females hunt significantly less than males do with females at Gombe being responsible for only 14.5% of all hunting kills (Gilby et al., 2017). Though they do participate in red colobus hunts occasionally, female chimpanzees exhibit more risk-averse behavior, typically focusing on smaller and more consistent prey items like bushbuck (Gilby et al., 2017).

3.2 Sex and Reproductive State

Access to energy is in part determined by an individual's diet quality, which limits reproductive success in female mammals (Gadgil and Bossert, 1970; Trivers, 1972). Long-term access to high quality resources for females is especially important when rate of reproduction and gestation is elongated, and when there is a lack of paternal investment in offspring, such as is the case for chimpanzees. During gestation and lactation, female mammals often increase their caloric intake by increasing the time they spend foraging and focus their efforts on high-quality foods (Lee, 1987; Gittleman and Thompson, 1988). In primates, lactation is accompanied by an increased energy intake for all species, while energy intake during pregnancy increases in some species, but not all (Dufour and Sauther, 2002).

Because of the energetic demands of pregnancy, a female chimpanzee's reproductive state also affects her dietary makeup. Pregnant chimpanzees gain up to 15% of their body weight during pregnancy (Pusey et al., 2005), heightening their energetic and caloric needs. To

maximize caloric intake during pregnancy, female chimpanzees have been observed increasing the quality of their diet by increasing fruit consumption (Murray et al., 2009). Access to high-quality fruit can also determine when chimpanzees reproduce. Studies on female chimpanzee reproductive timing confirm this, as reproductive cycles and rates of conception closely follow seasonality of high-energy, preferred food sources (Emery Thompson and Wrangham, 2008; Emery Thompson et al., 2007).

3.3 Female Hierarchy and Competition

Social dominance influences foraging success and thus energy intake in a variety of taxa. Higher-ranked individuals benefit by having priority of access to food resources (in geese: Stahl et al., 2001; in hyenas: Tilson and Hamilton, 1984), receiving greater amounts of energy from foraging (in salmon: Metcalfe, 1986; in capuchins: Vogel, 2005), and foraging on higher quality resources (in geese: Hupp et al., 1996; in pronghorns: Dennehy, 2001). Following this, the hierarchical component of chimpanzee group structure can play a large role in an individual's access to resources and diet quality. Competition between ingroup females, which is related to social dominance rank, has been observed to directly influence which group members have access to the highest quality foraging areas (reviewed in Pusey and Schroepfer-Walker, 2013).

Unlike males who rise through the community hierarchy by directly challenging higher-ranked individuals, female chimpanzees form consistent dominance hierarchies within a community based on a queue where direct challenging of another female is uncommon and rank placements are consistent over time (Foerster et al., 2016). A study on the Tai chimpanzees demonstrated that the most significant determinant of dominance rank was food contest success, and that both typically increased with age (Wittig and Boesch, 2003). In other words, dominance

rank and winning food contests increased as chimpanzees got older. This means that females that reach sexual maturity and immigrated into a new community are at a disadvantage compared to natal females. Newly sexually mature daughters of high-ranking females that remain in their natal community have opportunities to increase their rank compared to similarly aged immigrant females (Foerster et al., 2016). These opportunities occur both through the outright social implications of maternal presence as well as due to increased strength and competitiveness for core areas resulting from the long-term high diet quality provided by their mothers (Foerster et al., 2016).

Chimpanzee females with a higher dominance rank receive many benefits that are influenced by their ability to maintain high-quality food patches. High-ranking females acquire a suite of reproductive advantages, including shorter inter-birth intervals and better offspring survival (Pusey et. al, 1997). Similarly, high female competitiveness in Tai chimpanzees leads to shorter interbirth intervals (Lemoin et al., 2020). Even daughters of high-ranking females conferred reproductive benefits, such as sexually maturing at faster rates than daughters of lower-ranked females (Pusey et al., 1997; Walker et al., 2018).

Competition for food resources is a significant driver of competition among female chimpanzees. As previously mentioned, physical competition among female chimpanzees is rare when compared to males, but recent research has shed some light into the ways that females compete for food and space within a community. In addition to directly competing for food in individual patches, females compete for long-term access to core areas that contain higher densities of available fruit (Williams et al., 2002; Thompson et al., 2007; Miller et al., 2014). High-ranking females often have priority access to these areas, while low-ranking females avoid these areas and forage elsewhere, leading to more time spent in lower quality foraging areas and

a higher likelihood of facing food scarcity (Murray et al., 2006). Additionally, high-ranking females are known to forage higher in the canopy, where fruit quality is higher (Kahlenberg, 2006). High-ranking females also typically spend more time eating meat compared to lower ranked females (O'Malley et al., 2016). In addition, high dominance rank in female chimpanzees is associated with a better likelihood of maintaining a stable and overall larger body mass for (Pusey et al., 2005), and the quality of a female's core area has direct implications for reproduction (Thompson et al., 2007).

3.4 Immigration Status

Increased familiarity with a habitat site has several positive effects on fitness because residents can move more quickly through the habitat, evade predators, and manage social interactions with neighbors more efficiently (Piper 2011). More pertinently, familiarity with a site, and thus knowledge of resource distribution, has been observed to increase foraging efficiency in some taxa (in hummingbirds: González-Gómez and Vasquez, 2006; in penguins: Rebstock et al., 2022). In primates, exploration of a new area is correlated with a lower foraging efficiency of preferred foods (in mangabeys: Janmaat and Chancellor, 2010). Thus, immigrant chimpanzees who have lower levels of site familiarity within their new community after permanent dispersal potentially face decreased foraging efficiency and lower quality of diet.

In addition to the possible effects of site unfamiliarity, space use is also affected by negative interactions with resident females. Immigrant females enter the dominance rank queue at a lower position than natal females (Foerster et al., 2016), which leaves them susceptible to the many disadvantages that come with being a low-ranked chimpanzee female.

This includes decreased access to high quality core areas. These disadvantages are also exacerbated by the increased aggression toward immigrant females, who are trying to access feeding areas, from resident females who already inhabit high-quality, neighboring areas (Kahlenberg et al., 2008b). At Gombe, immigrant female chimpanzees avoid core areas typically inhabited by dominant females likely because of the increased aggression immigrant females might expect (Murray et al., 2006). In turn, immigrant females have less site fidelity and larger foraging areas, which means that they likely suffer from foraging inefficiency and lower-quality diets (Murray et al., 2006). Thus, the social repercussions that accompany immigration into a new community may lead to foraging disadvantages for female chimpanzees.

4. Conclusion

Therefore, in this study, the objective is to untangle the relationships between female chimpanzee reproductive stage, residence status, and diet quality, focusing specifically on the transition from the juvenile period into adolescence and through the first pregnancy. Few studies have focused on the foraging behavior of females during these major life transitions and no study to date has examined feeding behavior throughout stages of dispersal and into first pregnancy. Two hypotheses of the foraging behaviors of newly mature female chimpanzees at Gombe will be tested with special attention given to the females' reproductive state and immigrant status.

First, I will test the hypothesis that the social costs of dispersal will result in lower diet quality of immigrant female chimpanzees. Within this hypothesis, I predict that natal females will have a higher quality diet than immigrant females in sexual maturity, as higher-ranking females have greater access to higher quality foraging areas and resident females are usually higher ranked than immigrant females. Additionally, I predict that immigrant females will

exhibit less faunivory than natal females, as low-ranking females feed less on meat than resident females prior to first pregnancy. Then, I will analyze the hypothesis that the energetic and nutritional requirements of pregnancy will increase foraging effort in female chimpanzees. Here, I predict that primiparous pregnant females will spend more time foraging because of the higher energetic demands of pregnancy. Additionally, I predict that primiparous pregnant females will spend more time foraging for meat and insects than nonpregnant females because of the nutrients required to sustain a pregnancy.

METHODS

1. Study Location and Subjects

Data previously collected on female chimpanzees at Gombe National Park will be used to address the four predictions. Gombe National Park is located along the eastern edge of Lake Tanganyika in western Tanzania and covers 35 km^2 of diverse habitat including mountains, valleys, woodland, and grassland (Goodall, 1986). The area is seasonal, the dry season occurs from May-October and the wet season from November-April (Pusey et al., 2005). The park is home to three communities of wild eastern chimpanzees. Long-term studies have been conducted on the two habituated communities, the centrally located Kasekela and the northern Mitumba, since 1974 and 1994, respectively (Wilson, 2012). Chimpanzees in the two communities are individually recognized and maternal relationships are known. The third and southernmost community, Kalande, is not habituated but is known genetically, allowing researchers to track females who disperse between all three communities within the park.

Subjects included maturing females aged 10 - 20 years living in either habituated community between 2005 and 2017 that met the minimum observation requirement (see below; Table 1). Females were classified based on their reproductive and resident status into a category called “female status”. Females could be exclusively classified as sexually mature natal (SMN), sexually mature immigrant (SMI), or primiparous pregnant (PP).

Female chimpanzees are considered sexually mature at the age they have a full estrous swelling and first mate with a sexually mature male. This typically occurs at 11.5 years of age for the Gombe females (Walker et al., 2018). Females age out of this category when they conceive in their natal community or transfer to a new community. Once sexual maturity is reached and transfer into a new community is permanent, females are considered immigrants.

Once a female conceives within her permanent adult community, she is considered pregnant. Conception dates are estimated by subtracting the mean population gestation of 228 days (Feldblum et al., 2022) from the first infant's estimated birthdate. Due to the fission-fusion social system, females are not observed daily, so infant birthdates are assigned as the median between the date a female was last seen without an infant and the date she was first seen with an infant, except in cases were a more recent birth is indicated, such as an attached umbilicus. In this sample, median days between a female's last seen date without an infant and first seen date with an infant is 13 days (range 1 - 18).

When examining foraging during pregnancy, females were further classified by origin. Natal females are defined as those who were born into a community and stayed in the same community throughout adulthood. There is one exception, Eowyn, who immigrated into the Kasekela community when she was 3.8 years old but was classified as a natal female since the majority of her juvenile period was spent in Kasekela (Walker, 2015). Immigrant females were those that were born into one community and dispersed to another community during or after sexual maturity.

Because Gombe chimpanzees are tracked throughout all stages of life, some individuals were observed in multiple residence and reproductive states, as shown in Table 1. For example, Flirt (FLI) was born in Kasekela, but dispersed to Mitumba in adulthood. So, Flirt was observed as both a sexually mature natal female and a sexually mature immigrant female in the two communities, respectively. Because life stages were defined by behavioral milestones, chronological age within a category is variable. However, chimpanzees begin adopting adult-like feeding patterns including diversity of diet and time spent foraging before the onset of sexual

maturity (Lonsdorf et al., 2021). Therefore, diet quality should not vary significantly based on development or age-related maturity for the age range included in this study.

2. Data Collection

I gathered feeding behavior data on Gombe chimpanzees in the Kasekela and Mitumba communities from two focal feeding records, the Female Behavioral Development (FBD) database and the Gombe Stream Research Center (GSRC) database. The FBD project was created to collect data on young female chimpanzee development and follows maturing females exclusively. This record includes 23 young female chimpanzees including new immigrant females between the years of 2011 and 2018 (Walker, 2015). To increase the number of observation hours I included feeding data collected by GSRC from the years 2005 and 2017. Data collection by GSRC has been ongoing since 1973 but primarily focuses on adult males and resident females. Maturing females are not regularly followed by the GSRC team, but nevertheless, the GSRC database contains some focal follow data on 18 of the 23 females in the FBD database. Both the FBD and GRSC records collect focal data using the same methods. By combining the FBD record and the GSRC data, I accumulated 9,369 total hours of observation. From this, 4,415 hours of feeding bouts were collected on 23 young female chimpanzees in the Kasekela and Mitumba communities in Gombe National Park. To be included in the final dataset, a female must have been observed for at least 12 hours in each season. This resulted in a final dataset of 2,230 hours of total focal observations and 1,055 hours of feeding bout data from 14 young females between the years 2009-2018 (Table 1).

The two focal feeding records included data from multiple-hour focal follows in which observers noted the identity and estrous state (as determined by the degree or anogenital

swelling) of the individual and record behavior patterns including every feeding bout. The focal follows occur year-round in both the wet and dry seasons. In the FBD record, researchers conducted follows of individuals starting in the mornings at the previous night nest or whenever the individual was located by researchers, and ending when the individual was unable to be located further or at a previously determined time (Walker, 2015). The FBD record had a median focal length of 7 hours per focal. The GSRC researchers typically started and ended follows at the night nest and had a median focal length of 9.12 hours per focal. The researchers selected which female to follow each day by cycling through and not repeating an individual until every female chimpanzee had been followed when able. During each bout of foraging, the researchers noted the start and end time as well as the species of the food consumed. For plants, researchers also noted the part of the plant consumed by the chimpanzee. These parts are exclusively classified as fruits, leaves, pith, shoots, flowers, sap, bark, or fronds.

3. Foraging Metrics

I identified and calculated several diet measures to assess diet quality holistically following and expanding upon Murray et al. (2006). The resources that a chimpanzee has access to and chooses to spend time pursuing is complex and affected by many different factors, like dominance rank, age, sex, and nutritional needs. So, multiple measures are needed to evaluate quality from all sides instead of assessing a single measure.

Time spent foraging can be a measure of efficiency and effort by an individual. Time spent foraging for each female was calculated for each follow as

$$Total\ time\ spent\ foraging\ \div\ Total\ observation\ time$$

I also calculated the amount of time spent foraging on five different food groups: Top 24 preferred foods (specified below), fruit, leaves and pith, insects (invertebrate prey), and meat (vertebrate prey). Time spent feeding in each food group was calculated for each follow as

$$Total\ time\ spent\ foraging\ food\ group\ \div\ Total\ time\ spent\ foraging$$

Foerster and colleagues (2016) found that 24 plant species, mostly producing fleshy fruits that chimpanzees prioritize, make up 75% of Gombe chimpanzee diet. Therefore, these top 24 food species are of high dietary importance and more time spent foraging on these species indicates higher overall diet quality.

Chimpanzees are ripe fruit specialists and will always choose fruit when it is available, meaning food sources like leaves and pith are commonly considered fallback foods (Wrangham et al., 1998). Previous studies found that the amount of leaves and pith in the diet of Gombe chimpanzees correlate with lower body mass (Gilby et al., 2006). Thus, higher percentages of leaves and pith can be indicative of a low-quality diet (Walker, 2015). Meat and insects are important sources of nutrients and minerals for chimpanzees (Milton, 2003, Tennie et al., 2009, O'Malley and Power, 2012, O'Malley and Power, 2014), so a diet low in these items may also be considered of relatively lower quality.

Additionally, overall diet breadth was calculated as

$$Number\ of\ food\ species\ consumed\ \div\ Total\ observation\ hours$$

In ecological theory, a greater diet breadth is typically interpreted as a decrease in overall diet quality (Charnov, 1976).

4. Data Selection and Analysis

For a female chimpanzee to be included in the final data analyses, she must have been observed for 12 hours in a status category (SMN, SMI, or PP) in a given season and year. I analyzed female feeding data within seasons per year, so each data point is assigned a year and season. (e.g. 2017 dry season). Because of this, some females appear twice in the same season in different status categories. If a female spent 12 observed hours as SMN or SMI and then became pregnant and spent 12 observed hours as PP within the same season, she could be included twice in the same season as two separate data points. To account for this repetition, subject ID was considered in all analyses. The objective of this study was to analyze differences in feeding behavior after the onset of sexual maturity, so data on females in early adolescence were not included in the final model.

To assess differences in diet quality and composition among females of different reproductive states and residence status, while controlling for factors previously known or suspected to affect foraging, I used generalized linear mixed models (GLMM) and linear mixed models (LMM). These models allow for inclusion of both fixed effects and random effects that introduce variability into the data due to nonindependence (Bolker et al., 2009). For measures of diet quality that did not yield a proportion, I used a linear mixed model. This included diet breadth. Generalized linear mixed models are a more appropriate model for binary data, so I used GLMMs with a binomial distribution for measures of diet quality that yielded proportional data (Bolker et al., 2009). This included percentage of overall time budget spent foraging, and

percentage of time spent foraging on fruit, leaves and pith, meat, insects, and species in the top 24 food groups (cf. Foerster et al., 2016).

Each preliminary model included community, season, and female status (SMN, SMI, and PP) as potential main effects. After running the preliminary model, I would remove the variable with the highest p-value to find the model that best fit my data. I then used corrected Akaike Information Criterion (AICc) units to determine the quality of fit of my model, using a smaller AICc value as an indicator of a better fit (Hurvich and Tsai, 1989). The previous model was retained as the best fit for the metric if the model did not decrease by at least 6 AICc units, because a change of more than 6 AICc units enough improvement that model rejection should be considered (Symonds and Moussalli, 2011). Year and subject identification were included in each model as random effects to account for variability between individuals and years of data collection.

In addition, I conducted an analysis on solely PP females to analyze the effects of residential status (immigrant or natal) on feeding in a female's first pregnancy. Because the sample size was small for this analysis (12 data points), I only assessed one main effect and one random effect at a time within a model. In this analysis, I included residential status as a potential main effect and subject identification as a random effect.

I reported p-values, degrees of freedom, and F-values for each predictor that remained in the final model. A p-value of $p<0.05$ is considered significant, while a p-value of $p<0.1$ is considered a non-significant trend. When analyzing differences of means between predictor variables with more than two quantities (e.g. female status: SMN, SMI, and PP), I conducted post-hoc Tukey's honestly significant difference (HSD) tests and reported the p-values. The Tukey's HSD allowed me to test for significant differences between the means of all the groups

compared to one another. I also report the means and standard deviations for each foraging metric by each predictor variable. All statistical analyses for this study were performed using JMP version 16.0.0 (SAS Institute Inc., 2023).

Table 1. List of demographic information of subjects in final data analyses

Subject Identification	Years Observed	Female Status	Residence Status	Birth Community	Adult Community
GLD	2009-2011	SMN/PP	N	KK	KK
GLI	2010-2011	SMN/PP	N	KK	KK
EOW	2011-2014	SMN/PP	N	KK	KK
FLW	2015-2017	SMN/PP	N	MT	MT
FLI	2010-2015	SMN/SMI/PP	N/I	KK	MT
YAM	2011-2015	SMN/SMI/PP	N/I	KK	MT
SAM	2016-2017	SMN/SMI	N/I	KK	MT
EDE	2016-2018	SMN/SMI	N/I	MT	KK
MKW	2011-2014	SMI/PP	I	KL*	KK
CHE	2012-2013	SMI	I	UK	KK
OBE	2012-2013	SMI	I	KL*	KK
WEM	2014	SMI	I	UK	MT
LOS	2016-2017	SMI	I	MT	KK
KEA	2018	SMI	I	KK	MT

Female status: SMN = sexually mature natal, SMI = sexually mature immigrant, PP = primiparous pregnant
Residence status: N = natal, I = immigrant
Communities: KK = Kasekela, MT = Mitumba, KL = Kalande, UK = Unknown
* indicates community is suspected but not confirmed

RESULTS

1. Foraging Metrics by Female Status

Foraging metrics by female status are summarized in Table 2. Female status was found to be a significant predictor of the percentage of overall time observed feeding (p=0.03, Table 3). A post-hoc Tukey's HSD test found that primiparous pregnant (PP) females spent significantly more time foraging than sexually mature immigrants (SMI) (p=0.03, Figure 1). A similar trend emerged that sexually mature natal (SMN) females spent more time foraging than SMI, but failed to reach significance (p=0.06, Figure 1). Female status was not found to be a significant predictor of any other metric of diet quality in female chimpanzees. The percentage of top 24 foods, fruit, leaves and pith, meat, and insects in female chimpanzees' diet was not predicted by female status (Table 3, Figure 2, Figure 3). Furthermore, diet breadth was not significantly affected by any variable (Table 4).

Female status did not significantly affect faunivory. However, when examining the raw data descriptively, patterns of meat-eating varied by residence status. On average, SMI females ate meat less frequently than SMN females and PP females (Table 2, Figure 3), although the results were not significant (p=0.29, Table 3). Only two of the ten sexually mature females in their immigrant community were observed foraging on meat for a combined total of 72 minutes. By comparison, five of the eight sexually mature females observed in their natal community foraged on meat for a combined total of 700 minutes. Differences in meat-eating between immigrant and natal pregnant females are reported below. Consumption of insects did not vary across female status (Figure 3).

2. Foraging Metrics by Community and Season

Foraging metrics by community and season are summarized in Table 5. Community was found to be a significant predictor of the percentage of time spent feeding ($p<0.01$, Table 3). On average, Mitumba females spent 54% of their time foraging, while Kasekela females foraged for 40% of the time they were observed (Table 5). Community was not a predictor of any other foraging or faunivory metrics.

As expected, season was found to be a significant predictor for multiple foraging metrics (Table 3). Overall diet quality increased in the wet season: females spent more time consuming the preferred top 24 foods ($p<0.001$, Table 3) and spent less time foraging overall ($p=0.03$, Table 3). Although not significant, increased fruit consumption ($p=0.08$) and decreased insect consumption ($p=0.06$) occurred in the wet season (Table 3). Meat consumption was not significant but did decrease in the wet season ($p=0.14$, Table 3), but this may be due to a small sample size.

3. Foraging Metrics by Residence Status in Pregnant Females

Foraging metrics in pregnant females by residence status are summarized in Table 6. When individual chimpanzee identification was controlled for, residence status was found to predict a trend in meat consumption. This result was nearly significant, with pregnant immigrant females spending more time foraging for meat than pregnant natal females ($p=0.05$, Figure 4). Residence status did not predict any other foraging metric in pregnant female chimpanzees

Table 2. Observed means and standard deviations for foraging and faunivory metrics across female status.

	Female Status		
Foraging Metric	Sexually Mature Natal	Sexually Mature Immigrant	Primiparous Pregnant
Time Foraging (%)	45.5 ± 12.8	39.2 ± 15.2	52.9 ± 13.6
Fruit (%)	62.6 ± 17.9	64.7 ± 13.0	59.7 ± 17.8
Leaves and Pith (%)	12.7 ± 12.0	10.0 ± 8.7	18.7 ± 11.1
Top 24 (%)	70.0 ± 16.2	73.7 ± 12.1	70.3 ± 12.7
Diet Breadth	59.9 ± 22.8	61.8 ± 22.3	68.7 ± 17.6
Faunivory Metric			
Meat (%)	2.1 ± 3.41	0.3 ± 1.28	1.9 ± 2.78
Insect (%)	7.0 ± 8.92	6.1 ± 7.43	6.2 ± 7.16

Table 3. P-values, degrees of freedom, and F-values reported from generalized linear mixed models for foraging and faunivory metrics.

	Explanatory Variables		
Foraging Metric	Female Status	Community	Season
Time Foraging (%)	**p=0.028**** denDF=25.73 numDF=2 F-val=4.14	**p=0.006**** denDF=24.56 numDF=1 F-val=9.11	**p=0.030**** denDF=39.96 numDF=1 F-val=5.10
Fruit (%)		p=0.121 denDF=16.92 numDF=1 F-val=2.67	**p=0.077*** denDF=49.39 numDF=1 F-val=3.26
Leaves and Pith (%)	p=0.156 denDF=10.29 numDF=2 F-val=2.23	p=0.680 denDF=17.38 numDF=1 F-val=0.18	p=0.146 denDF=37.35 numDF=1 F-val=2.20
Top 24 (%)			**p=0.0003**** denDF=51.64 numDF=1 F-val=14.80
Faunivory Metric			
Meat (%)	p=0.291 denDF=16.46 numDF=2 F-val=1.33	p=0.575 denDF=2.43 numDF=1 F-val=0.41	p=0.138 denDF=47.04 numDF=1 F-val=2.28
Insect (%)		p=0.285 denDF=4.34 numDF=1 F-val=1.63	**p=0.057*** denDF=43.31 numDF=1 F-val=3.86

* indicates trend with p<0.1 and ** indicates significance with p<0.05. Gray boxes indicate that the variable was not retained in the final model.

Table 4. P-value, degrees of freedom, and F-value reported from linear mixed models for diet breadth.

Foraging Metric	*Explanatory Variables* Female Status	Community	Season
Diet Breadth		p=0.236 denDF=2.07 numDF=1 F-val=2.74	

Gray boxes indicate that the variable was not retained in the final model.

Table 5. Observed means and standard deviations for foraging and faunivory metrics across community and season.

	Community		*Season*	
Foraging Metric	Kasekela	Mitumba	Wet	Dry
Time Foraging (%)	40.2 ± 13.2	53.8 ± 12.7	42.5 ± 13.0	48.1 ± 15.7
Fruit (%)	59.6 ± 17.7	67.7 ± 11.9	66.7 ± 17.5	58.0 ± 12.7
Leaves and Pith (%)	13.8 ± 13.0	12.1 ± 6.9	11.0 ± 11.9	15.7 ± 9.8
Top 24 (%)	70.6 ± 13.4	72.4 ± 15.3	77.4 ± 9.87	64.4 ± 14.9
Diet Breadth	67.6 ± 22.7	53.8 ± 15.9	62.8 ± 23.4	62.3 ± 19.4
Faunivory Metric				
Meat (%)	1.4 ± 2.98	1.7 ± 2.54	0.9 ± 2.01	2.2 ± 3.41
Insect (%)	7.5 ± 9.31	4.7 ± 4.27	4.4 ± 6.37	8.8 ± 8.93

Table 6. Observed means and standard deviations of foraging and faunivory metrics across residence status for pregnant females only.

	Residence Status	
Foraging Metric	Natal	Immigrant
Time Foraging (%)	48.5 ± 10.8	58.0 ± 15.7
Fruit (%)	59.3 ± 19.1	60.3 ± 17.9
Leaves and Pith (%)	18.1 ± 11.7	19.3 ± 11.5
Top 24 (%)	71.3 ± 11.2	69.1 ± 15.2
Diet Breadth	77.4 ± 18.0	58.6 ± 11.2
Faunivory Metric		
Meat (%)	0.9 ± 2.09	3.2 ± 3.14
Insect (%)	7.3 ± 8.29	4.8 ± 6.04

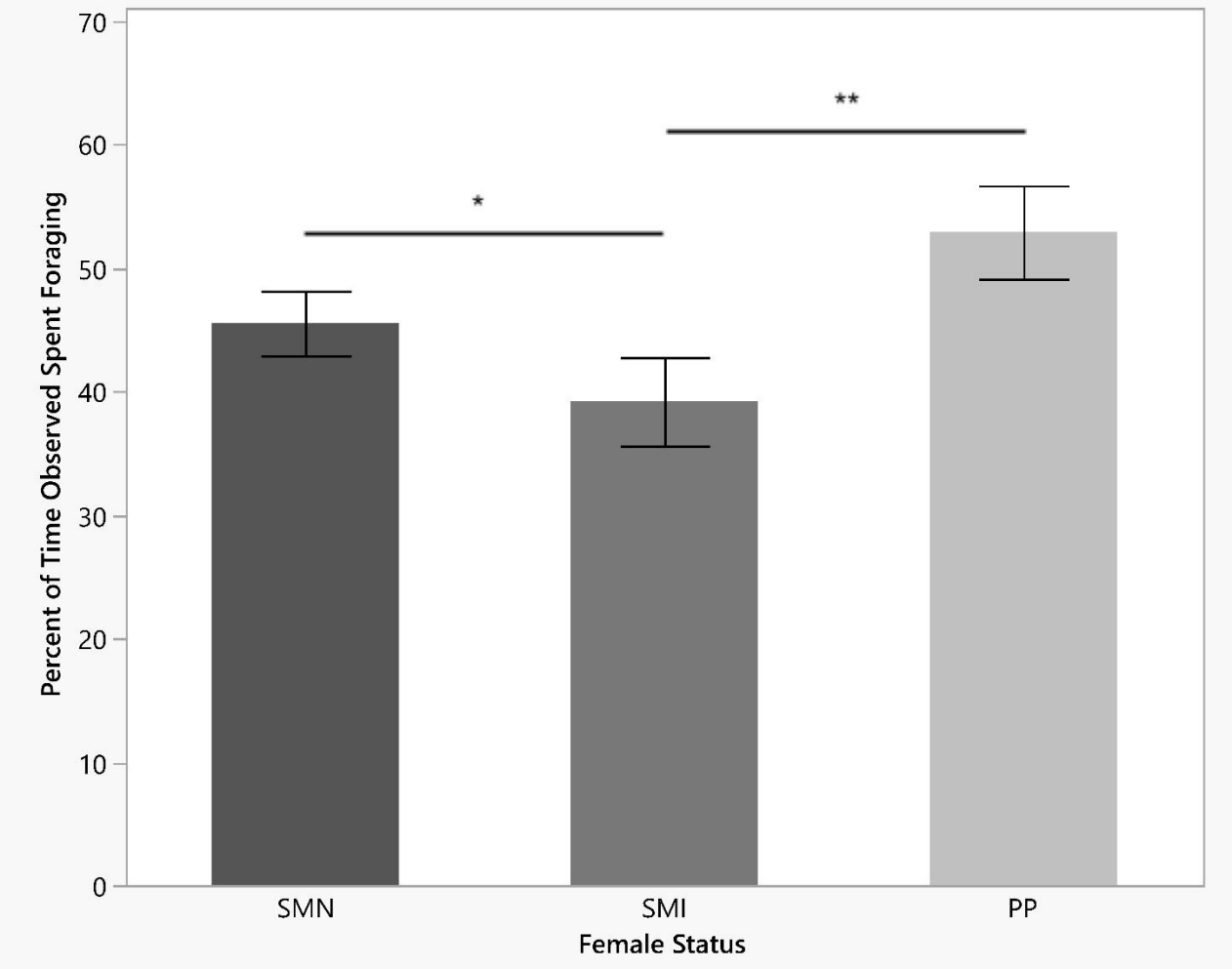

Figure 1. Mean percentage of overall time observed spent foraging across female status. Error bars represent the standard error. * indicates a pairwise difference with $p<0.1$ and ** indicates a pairwise difference with $p<0.05$ determined by pairwise Tukey's HSD tests.

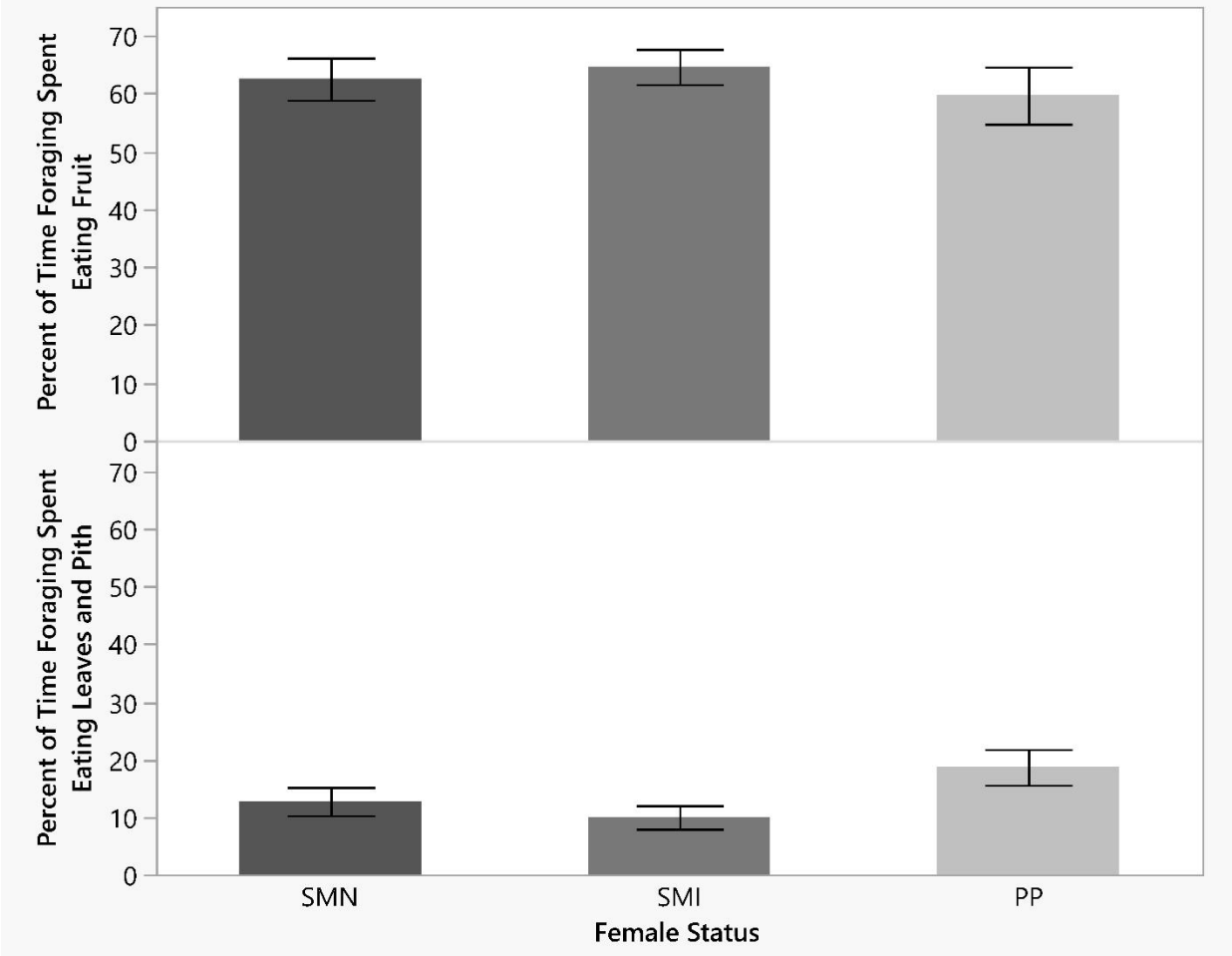

Figure 2. Mean percentage of overall time foraging spent eating fruit and leaves and pith across female status. Error bars represent the standard error.

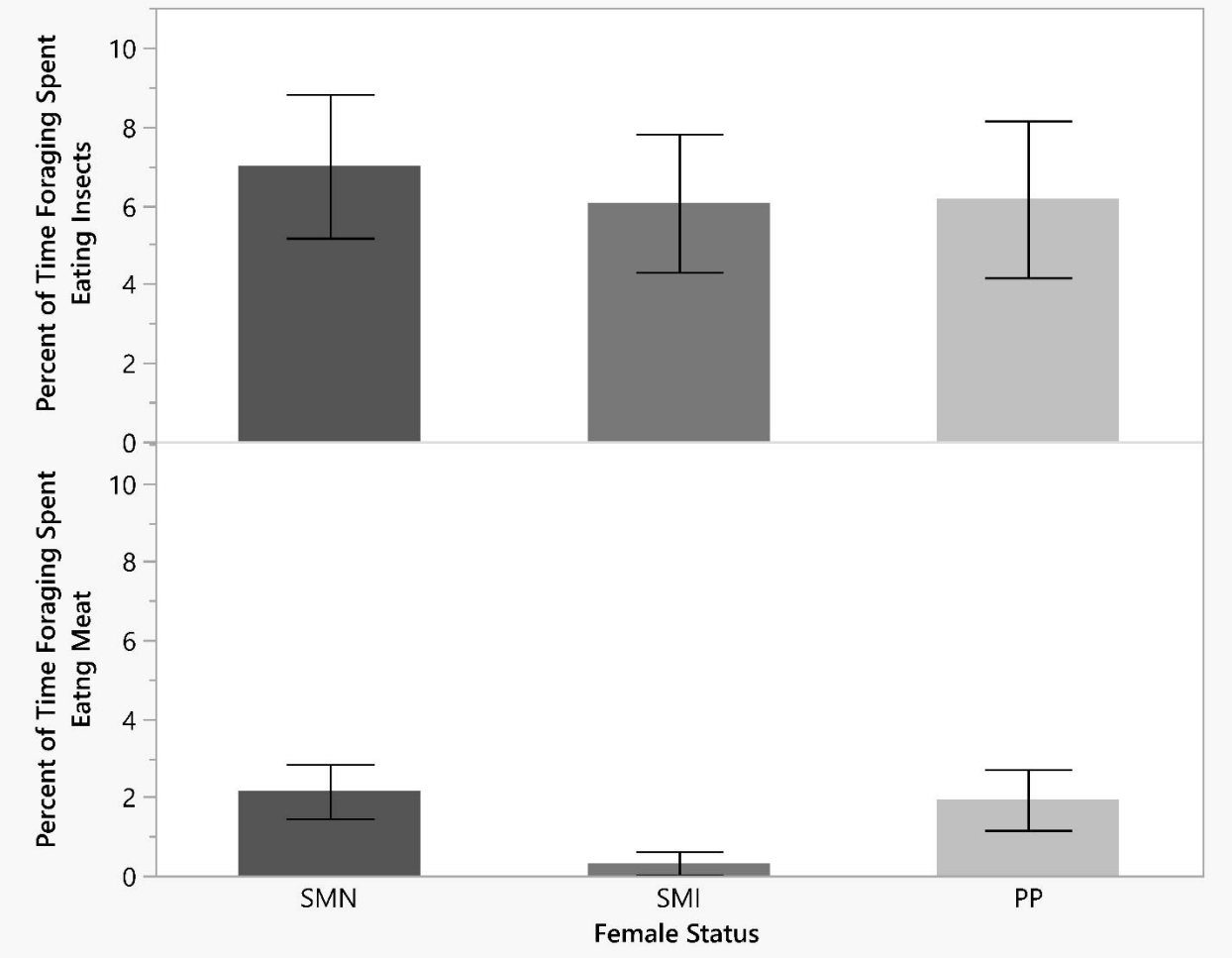

Figure 3. Mean percentage of time foraging spent eating insects (top) and meat (bottom) across female status. Error bars represent the standard error.

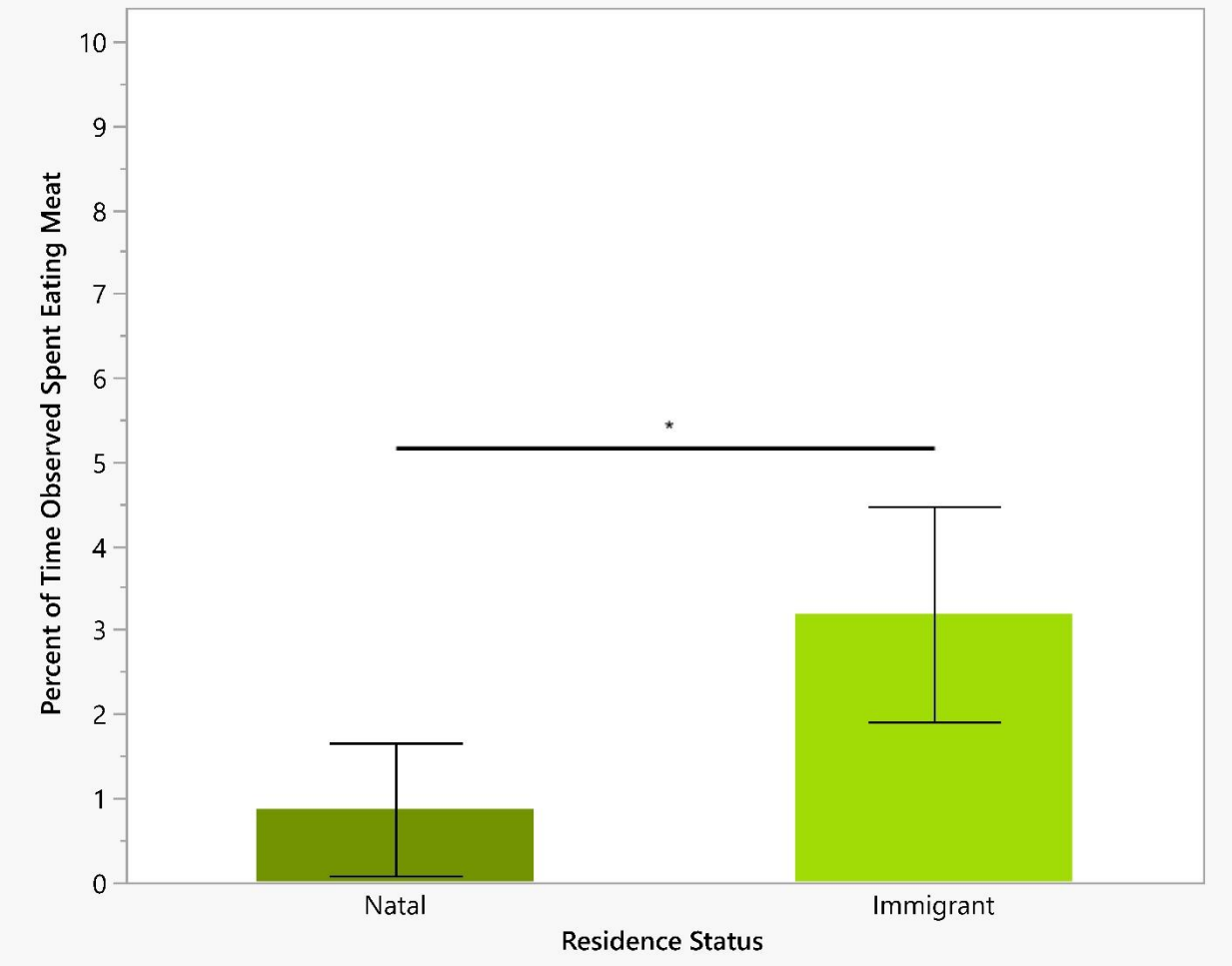

Figure 4. Mean percentage of time foraging spent eating meat across residence status in pregnant females only. Error bars represent the standard error. * indicates a pairwise difference with $p<0.1$ determined by pairwise Tukey's HSD tests.

DISCUSSION

Interestingly, I found that many foraging behaviors of young female chimpanzees did not appear to be affected by reproductive or residential status. For example, the percentages of fruit, leaves and pith, insects, and preferred top 24 foods were not found to significantly differ between primiparous pregnant and sexually mature natal and immigrant females. However, other foraging behaviors such as time spent foraging and meat consumption do appear to vary based on these factors.

Two trends of foraging behavior variation did emerge amongst sexually mature (SM) natal and immigrant females, though these both failed to reach statistical significance. SM immigrant females tended to spend less time foraging compared to their natal counterparts. Similarly, SM immigrant females spent a much smaller amount of time foraging on meat. In the latter case, it is worth considering that statistical significance regarding meat foraging bouts is difficult to assess due to their low overall frequency in female chimpanzees.

Once immigrant chimpanzees experience their first pregnancy, however, it seems as though these gaps begin to close. Primiparous pregnant females spent significantly more time foraging than SM immigrant females, but a similar amount of time foraging compared to SM natal females. When examining primiparous pregnant females only, the percentage of time spent foraging did not vary between immigrant and natal females. So, it seems that natal females spend a consistent amount of time foraging before and after first pregnancy, while immigrants experience a deficit after dispersal and must increase their foraging time to reach the baseline once pregnant. Similarly, an analysis of primiparous pregnant females found that pregnant immigrants ate an almost significantly increased amount of meat compared to pregnant natal females. Overall, these results seem to suggest that differences in foraging behavior following

dispersal in immigrant females (reduced time foraging, reduced meat consumption) compared to natal females may resolve before or upon first pregnancy.

1. Reproductive Status

In female mammals, the energetic requirements of pregnancy can influence behaviors that increase caloric intake, such as increasing the amount of time spent foraging or focusing efforts on high quality foods (Lee, 1987, Gittleman and Thompson, 1988). In this study, I found mixed support for the prediction that female chimpanzees would exhibit higher foraging effort during primiparous pregnancy. Gombe female chimpanzees in their first pregnancy did spend significantly more time foraging than SM immigrants, but a similar amount of time foraging compared to SM natal females. When observing pregnant females, no difference emerged between pregnant natals and immigrants. So, an increase in the time spent foraging was driven solely by immigrant females, who increased their foraging time once pregnant.

This finding partially contradicts results from a past study at Gombe, which found that non-pregnant, non-lactating adult females spent more time feeding when compared to pregnant females (Murray et al., 2009). The difference in findings may be explained by the current study's focus on the period beginning at sexual maturity and ending at completion of first pregnancy. In contrast, Murray's study contained all adult females within the community. The comparatively higher time spent foraging in the study of primiparous pregnant females suggests that female chimpanzees may exhibit higher foraging effort during first pregnancies compared to later ones. A higher maternal investment in first offspring has been previously observed in female chimpanzees at Gombe. The interbirth interval following a female chimpanzee's first pregnancy is longer than subsequent interbirth intervals (Jones et al., 2010), which can be interpreted as

higher maternal investment. In addition, primiparous Gombe mothers expended more effort with their first offspring during the first year of life by spending more time grooming, playing, and nursing their infants than multiparous mothers (Stanton et al., 2014). However, this pattern has not been observed during gestation, as gestation length in first and subsequent births does not differ in female chimpanzees (Feldblum et al., 2022). So far, no study has investigated differential maternal investment in the form of foraging behavior during gestation in chimpanzees. Future studies should focus on foraging during pregnancy and throughout individual females' lives to determine whether there are differential foraging behaviors during a female's first pregnancy compared to subsequent ones.

Another possible explanation for increased foraging effort during first pregnancy is that female chimpanzees continue to gain mass until around the age of 21 (Pusey et al., 2005), while the pregnant females included in this study had an average age of 15. It is possible that the higher foraging efforts of primiparous mothers in this study is correlated with age and the general energetic requirements of growth during early adulthood rather than higher maternal investment during their first gestation.

Additionally, travel costs associated with pregnancy may affect how primiparous pregnant females allocate their feeding time. Higher energetic demands of gestation may be mitigated by allocating energy away from some activities, like travel (Gittleman and Thompson, 1988). Pregnant females in Gombe spend less time traveling compared to females in other reproductive states, possibly to conserve fat in preparation for lactation (Murray et al., 2009). This may suggest that reducing travel and instead increasing consumption of available resources nearby may be a viable strategy to increase caloric intake for female chimpanzees in their first pregnancy.

2. Residential Status

Interestingly, the observed difference in total foraging effort between sexually mature and pregnant females was driven primarily by immigrant females. Natal females spent a similar percentage of their total time budget foraging in sexual maturity and during first pregnancy, while immigrant females increased their foraging during first pregnancy. Curiously, the current study found no difference in the proportion of any food group or in overall diet breadth between natal and immigrant females, suggesting that composition of diet is the same regardless of residential status during sexual maturity, but that new immigrants are just foraging for less time overall.

The decreased time that SM immigrants spent foraging compared to SM natal and primiparous pregnant females may be explained by an increased amount of time avoiding resident females. An immigrant female entering a community introduces competition for resident females over resource-bearing core areas and possibly mates (Schroepfer-Walker and Pusey, 2013). Aggression between female chimpanzees is known to be rare, but evidence of aggression from resident females to incoming immigrants has been documented at every studied chimpanzee population. Because of the fission-fusion grouping system, immigrant females can avoid associating with certain individuals and have been observed avoiding dominant females in shared areas (Murray et al., 2009), likely to avoid aggression. So, immigrants may be spending more of their time avoiding or defending themselves from resident females and less time foraging compared to natals.

The deficit in foraging time for SM immigrants may also be explained by a higher amount of time spent in association with males. Immigrant female chimpanzees are known to travel and associate with males more than resident females even outside of sexual cycling for

protection against intrasexual aggression (Kahlenberg et al., 2008a). Because chimpanzees are known to spend less time foraging when in parties (Wrangham and Smuts, 1980), this may explain why SM immigrants foraged for less time than SM natal and primiparous pregnant females.

Even though SM immigrants spent less of their time feeding, their overall diet composition remained similar to SM natals and primiparous pregnant females. The lack of observed diet quality decrease when female chimpanzees immigrate may be a result of flexible integration tactics prior to permanent dispersal that increase familiarity with resources in the new community and thus lessen energetic costs. For example, females may begin to transfer by dispersing into a new community socially, but still utilize familiar food resources in their natal community (Isbell and van Vuren, 1996), a phenomenon that has been previously observed in the females at Gombe (Walker, 2015). Additionally, female chimpanzees are known to visit new communities prior to dispersal when in estrous and thus attractive to resident males, allowing them to become familiar with foraging resources (Walker, 2015). Through these tactics, diet composition may be retained, and energetic costs may be mitigated once permanent dispersal occurs.

Differences in time observed foraging between immigrants and natal females are also likely impacted by bias in the study design and a lack of control for group size. Because natal females and their ranging patterns are typically familiar to field researchers, they are more likely to successfully follow a natal female when she is foraging alone. In contrast, females who have recently immigrated into a community have unfamiliar ranging patterns, are wary of close observation and are especially skittish, all of which combine to hamper observations when alone. Consequently, immigrants are much more likely to be observed foraging within a large party

than on their own. Chimpanzees are known to spend less time foraging in parties (Wrangham and Smuts, 1980), so this bias may partially explain why SM immigrants spent less time foraging than other groups in the current study.

3. Faunivory

Nutrients found in animal flesh and insects may be especially important during pregnancy for chimpanzees. In humans, mineral deficiencies during pregnancy can lead to reproductive consequences such as birth defects, preterm birth, and loss of pregnancy (Gernand et al., 2016). Therefore, the trace nutrients that meat can provide for chimpanzees may aid in carrying a healthy pregnancy (Tennie et al., 2009). Increased faunivory has also been correlated with higher reproductive success in chimpanzees, as evidence suggesting a correlation between the consumption of meat and higher reproductive success among female chimpanzees has been presented by McGrew (1992). Similarly, Gombe females who fished for termites more often have been found to exhibit higher levels of lifetime reproductive success (Mackworth-Young and McGrew, 2014). However, these relationships may not be directly causal and instead explained by dominance rank, as higher rank correlates with higher reproductive success (Pusey et al., 1997) and access to meat (O'Malley et al., 2016). To untangle the relationships between these factors, future studies should analyze levels of faunivory in female chimpanzees and reproductive success while also controlling for dominance rank.

Though not statistically significant, I found that SM immigrant females had lower rates of meat consumption compared to SM natal females when examining the raw data descriptively. When analyzing pregnant females, a trend did emerge showing increased meat consumption in pregnant immigrant females when compared to pregnant natal females. This suggests that meat

consumption of immigrant females is low directly after dispersal but increases during first pregnancy, while meat consumption in natal females remains consistent regardless of reproductive status. Thus, pregnant immigrant females may be specifically compensating or resolving low levels of meat consumption prior to or upon first pregnancy, a time where acquiring nutrients found in meat may be crucial to reproductive success.

In previous studies analyzing faunivory in female chimpanzees at Gombe, meat-eating was found to vary by reproductive status, but only in low-ranking females (O'Malley et al., 2016). O'Malley found that meat intake among high-ranking females remained consistent despite pregnancy, but that low-ranking females increased meat consumption during pregnancy compared to a baseline state. Because young females that have recently immigrated into a new community are more likely to hold a lower dominance rank compared to natal females (Foerster et al., 2016a), this phenomenon may also be observed in the current study if immigrant females are considered low-ranking and natal females are high-ranking in comparison.

Because meat is a resource highly controlled by males, female access to meat may be influenced by a few social factors. The results of this study do not provide evidence for the "meat-for-sex" hypothesis, at least in the context of young females, as levels of meat consumption remain somewhat consistent across reproductive status. This supports a previous lack of evidence of chimpanzee females using sexual access as transactional for meat (Mitani and Watts, 2001, Gilby et al., 2010). The disparity between meat intake of SM natals and SM immigrants may instead be explained by male carcass-holder's higher social tolerance toward higher-ranked females compared to low-ranked females, as suggested by O'Malley.

Another possible explanation for immigrant females increasing meat consumption upon first pregnancy may be their increased willingness to beg carcass-possessing males for meat once

pregnant. Because resident females are known to express aggression toward new immigrants upon transfer (Kahlenberg et al., 2008a, Pusey et al., 2008), it is possible immigrants are less likely to beg for meat in a social setting where resident females are also begging. In Kasekela, low-ranking females have been found to associate least often with dominant females, even when they reside in the same neighborhood (Murray et al., 2006), which suggests possible avoidance of dominant residents by subordinates. However, once the immigrant female becomes pregnant, she has then had more time to form more stable social bonds and may not be as hesitant to beg. It is also possible that the nutrients that are provided by meat are so important for a successful pregnancy that she is more willing to beg even if it means assuming the risk of confronting a possibly aggressive resident female.

Although some trends were noted in this study, this dataset is adversely affected by a small sample size due to the infrequency of meat consumption in female chimpanzees. Many of the subjects, including natal females, were not observed eating meat within a season at all, making identifying trends difficult. The sample size for the analysis of meat consumption in pregnant females was extremely low, with only four natal females and three immigrant females being represented. Future studies with larger datasets may illuminate more on the social patterns of meat eating among immigrant and natal females, as well as the importance of meat consumption during subsequent pregnancies and the energetically expensive period of lactation.

Unlike the trends found in meat consumption, insect consumption did not vary with reproductive and residential status. This supports previous findings and suggests that within-community competition between females does not grossly affect insect consumption (O'Malley et al., 2016). This could be because insect resources may be more equally distributed across the community and are not highly guarded by males or high-ranking females like carcasses and fruit

patches are (Murray et al., 2006, Gilby et al., 2017). Interestingly, there was no observed trade-off between meat and insect consumption observed in this study. Sexually mature immigrants, who ate less meat than the other groups of females, did not consume more insects to make up for their lack of meat consumption. The macronutrients of vertebrate and invertebrate chimpanzee prey are known to be similar (Tennie et al., 2014), so it is possible that meat and insects serve different roles as sources of micronutrients for chimpanzees.

4. Season

As expected, season was found to greatly impact diet composition in young females, with overall higher diet quality occurring in the wet season and evidence of food scarcity occurring in the dry season. Because the high-energy ripe fruits that chimpanzees prefer are typically seasonally available, absences of these fruits can cause competition over high-quality foraging patches and food scarcities (Conklin-Brittain et al., 1998; Wrangham, 2000). I found that young female chimpanzees compensate for seasonal food scarcities by spending more time foraging overall, decreasing foraging effort on preferred foods, and increasing foraging efforts on low-quality fallback foods like leaves and pith in the dry season compared to the wet season. These results support similar findings of female chimpanzees in Gombe seasonally broadening their diet breadth and increasing foraging efforts to adapt to periods of food scarcity (Murray et al., 2006).

Season also seems to influence faunivory in female chimpanzees, although much less significantly than other measures. Female chimpanzees spent marginally higher percentages of foraging effort on meat and insects in the dry season than the wet season, perhaps signifying that they may be used as fallback foods in times where fruits are less readily available. The hunting

of red colobus monkeys is known to be seasonal at Gombe, occurring in the dry season, but other chimpanzee populations have peak hunting seasons during the wet season (Stanford, 1994). Most insect species at Gombe, including ants, are available throughout the year regardless of season (O'Malley and Power, 2014), which may make them more reliable food sources compared to fruit. However, termite-fishing does peak in the early wet season based on increased termite activity (Goodall, 1986), so it seems that many factors impact seasonal patterns of faunivory. Regardless, patterns of faunivory are difficult to untangle definitively with a small sample size. Future studies with more long-term data on faunivory should investigate the energetic importance of meat and insect consumption for female chimpanzees around reproductive age during periods of food scarcity.

5. Community

Although the community that the subject resided in did not affect the proportion of different foods present in overall foraging budgets, females in the community of Mitumba spent a significantly larger proportion of their time foraging when compared to Kasekela females. This could be a function of the differential sizes of the communities, as Kasekela has a much larger population and is spread over a large area of land compared to Mitumba (Wilson, 2012). Mitumba's overall smaller population may lead to the presence of regularly smaller foraging parties or larger amounts of isolated foraging time for young females compared to Kasekela. This may explain the disparity in overall foraging effort, as individuals in smaller foraging parties have been found to spend more time foraging compared to those in larger foraging parties (Isabirye-Basuta, 1988).

6. Conclusion

In summary, a holistic analysis of diet quality in female chimpanzees found that diet composition does not vary significantly between primiparous pregnant and sexually mature natal and immigrant females. I found evidence that dispersal resulted in some dietary costs for immigrant female chimpanzees, as sexually mature immigrants tended to spend less time foraging and may have consumed less meat than immigrants, but these results were not significant. However, dietary composition stayed consistent between sexually mature immigrant and natal females, likely because immigrant females utilize integration tactics before permanently dispersing into a new community to maintain consistent diet quality. I found mixed evidence for the hypothesis that primiparous pregnancy increases foraging effort in newly mature female chimpanzees. Primiparous pregnant females did feed for longer times, but only compared to sexually mature immigrants. Dietary changes between sexual maturity and first pregnancy occurred exclusively in immigrants, suggesting that immigrants face dietary deficits after dispersal that warrant improvement before or upon first pregnancy. In contrast, the diets of natal females remain consistent regardless of reproductive status and do not exhibit such deficits. Although the sample size of this study was small and thus limited some statistical analyses, it provides a starting point for future studies to continue understanding the effects of dispersal and first pregnancy on foraging behavior in newly mature female chimpanzees.

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