The Behavioural Ecology of the Northern Muriqui (*Brachyteles hypoxanthus*) at the Reserva Particular Patrimônio Natural-Feliciano Miguel Abdala (RPPN-FMA), Minas Gerais, Brazil.

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Table of Contents

List of Tables

List of Figures

List of Appendices

Appendix I: The output of the general linear model (activity budget); specifically, the analysis of variance. Displayed here are the degrees of freedom (DF), F-Value, and P-Value.

Appendix II: Tukey Pairwise Comparisons of the sample periods (activity budget) (grouping information using the Tukey Method and 95% confidence) are listed below to show where the significant differences were over the sample periods (sorted by the highest mean in descending order). Means that do not share a letter are significantly different.

Appendix III: The output of the general linear model (activity budget; age-sex class differences); specifically, the analysis of variance. Displayed here are the degrees of freedom (DF), F-Value, and P-Value.

Appendix IV: Tukey Pairwise Comparisons of the subsets (activity budget; age-sex class differences) (grouping information using the Tukey Method and 95% confidence) are listed below to show where the significant differences were between the subsets (sorted by the highest mean in descending order). Means that do not share a letter are significantly different.

Appendix V: The output of the general linear model (feeding time analysis); specifically, the analysis of variance. Displayed here are the degrees of freedom (DF), F-Value, and P-Value.

Appendix VI: Tukey Pairwise Comparisons of the sample periods (feeding time analysis) (grouping information using the Tukey Method and 95% confidence) are listed below to show where the significant differences were over the sample periods (sorted by the highest mean in descending order). Means that do not share a letter are significantly different.

Appendix VII: The output of the general linear model (feeding time analysis with maturity stated); specifically, the analysis of variance. Displayed here are the degrees of freedom (DF), F-Value, and P-Value.

Appendix VIII: Tukey Pairwise Comparisons of the sample periods (feeding time analysis with maturity stated) (grouping information using the Tukey Method and 95% confidence) are listed below to show where the significant differences were over the sample periods (sorted by the highest mean in descending order). Means that do not share a letter are significantly different.

Appendix IX: The output of the general linear model (feeding time analysis; age-sex class differences); specifically, the analysis of variance. Displayed here are the degrees of freedom (DF), F-Value, and P-Value.

Appendix X: Tukey Pairwise Comparisons of the groups (feeding time analysis; age-sex class differences) (grouping information using the Tukey Method and 95% confidence) are listed below to show where the significant differences were between the groups (sorted by the highest mean in descending order). Means that do not share a letter are significantly different.

Appendix XI: The output of the general linear model (feeding time analysis with maturity stated; age-sex class differences); specifically, the analysis of variance. Displayed here are the degrees of freedom (DF), F-Value, and P-Value.

Appendix XII: Tukey Pairwise Comparisons of the groups (feeding time analysis with maturity stated; age-sex class differences) (grouping information using the Tukey Method and 95% confidence) are listed below to show where the significant differences were between the groups (sorted by the highest mean in descending order). Means that do not share a letter are significantly different.

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Abstract

The northern muriqui (*Brachyteles hypoxanthus*) is a critically endangered species of primate endemic to the Brazilian Atlantic Forest. Strier collected data on the behavioural ecology of the Matão group between 1983-84 at the Reserva Particular Patrimônio Natural-Feliciano Miguel Abdala (RPPN-FMA), Minas Gerais, Brazil. Data on the behavioural ecology of the Jaó group were collected at RPPN-FMA between 2003-04. All methodology used for behavioural data collection of the Jaó group followed methods implemented by Strier in her PhD thesis. The Matão's and Jaó's behavioural ecology was compared in this thesis. The Jaó group was more than three times the size of the Matão group during the respective study periods. The Jaó group devoted more time to feeding, socialising, and engaging in "other" activities; whereas, the Matão group devoted more time to resting, travelling, and vocalising. The Jaó group devoted more time to feeding on fruits and flowers than the Matão group; whereas, the Matão group devoted more of their time feeding on leaves than the Jaó group. There was intermonthly variation in the Jaó group's activity budget, feeding time analyses, diurnal activity cycles, and day range travel lengths. The Matão group only exhibited intermonthly variation in their feeding time analyses and diurnal activity cycles. Greater intragroup feeding competition likely contributed to the larger Jaó group devoting more of their time to feeding and less time to resting than the smaller Matão group, and also why they spent more time feeding on food types at less preferable stages of maturity. In smaller groups with less intragroup feeding competition, adult females and adult males are able to spend the same amount of time feeding overall because adult females can spend more of their time feeding on high quality food resources (in the Matão group, adult females spent more time feeding on flowers than the adult males). As group size increases and intragroup feeding competition for preferred food resources increases, adult females have to spend more time

feeding overall (in the Jaó group, adult females spent more time feeding overall than the adult males). Perhaps differences in the two group’s home range habitat quality influenced activity budgets, as the smaller Matão group unexpectedly spent more time travelling. Differences in home range habitat quality could also explain why the Jaó group spent more time feeding on more desirable food resources, comparatively, than the Matão group. The influence of demographic differences undoubtedly also contributed to the behavioural differences that were presented here (the RPPN-FMA population grew from ~50 to >200 individuals, and from two to four groups between study periods). For the purposes of this thesis demographics are not of great focus but are discussed. Differences in rainfall, climatic conditions, and resource availability may have also influenced these results. This type of study is important because it provides insights into how different sized groups adapt their behavioural patterns in order to fulfil their energetic needs. Seasonal shifts in resource availability appears to place a greater stress on groups of larger sizes. Smaller groups may be able to maintain their activity budget year round, something larger groups may be unable to do. Implications for conservation include providing more evidence that even by 2003-04 the population at RPPN-FMA was closer to carrying capacity than it was in 1983-84. Habitat expansion, if possible, would be highly beneficial to the long-term health of the population.

1. Introduction

In this thesis the term "population" is used to describe all muriquis at a given locality (e.g. RPPN-FMA), unless specifically stated as the "entire population" which describes all muriquis (northern and southern species combined) from each known locality, or "entire population of northern muriquis" which is species specific. The term "group" is used to describe a subset of a population (e.g. Matão or Jaó group, both part of the RPPN-FMA population).

Muriquis (*Brachyteles* spp.) are endemic to the Brazilian Atlantic Forest. Listed as "critically endangered", it is estimated that the remaining size of the entire population amounts to fewer than 2,200 individuals which are now unevenly distributed among isolated forest fragments (Strier *et al.* 2017; Ferraz *et al.* 2019; Talebi *et al.* 2019). The Atlantic Forest now amounts to somewhere in the range of just 11.4-16% of its original size (Ribeiro *et al.* 2009).

The entire population of northern muriquis (*Brachyteles hypoxanthus*) is estimated at less than 1,000 individuals, making them the most threatened species in the *Brachyteles* genus (Ferraz *et al.* 2019). Currently, the largest known remaining population of northern muriquis is found at the Reserva Particular Patrimônio Natural-Feliciano Miguel Abdala (RPPN-FMA) in Caratinga, Minas Gerais, Brazil. Over 300 northern muriquis are living in this 1,000 ha Atlantic Forest Reserve (Lima *et al.* 2019).

This thesis compares the behavioural ecology of the Matão group from 1983-84 (Strier, 1987a; Strier, 1987b; Strier, 1991) with that of the Jaó group from 2003-04 to provide insights into how group size, resource availability, population density, and demographics can affect the behavioural ecology of northern muriquis.

The RPPN-FMA population has been continuously monitored since 2002, in particular, the Matão group has been studied almost continuously since 1982 by Dr Karen Strier (Strier & Boubli, 2006). The population and number of groups at the RPPN-FMA had more than doubled between study periods. At the time of Strier's study there were just two groups, Matão and Jaó, and Strier estimated the population was around 50 individuals. The population size was small during 1983-84 and Strier suggested that the Matão group, with just 26 individuals at the onset of her study, may have been living below carrying capacity (Strier, 1991). From 2003-04, almost 20 years after the Matão group was first studied by Strier, the Jaó group was systematically studied in an attempt to broaden the scope of information in regard to the behavioural ecology of a different group of muriquis living at the RPPN-FMA and in turn produce comparable data with that of Strier's. By the time of data collection for this study there were four groups (M2 group formed between 1988-1991 (Strier *et al.* 1993) and the Nadir group began to form in 2002 (Boubli *et al.* 2005)) and the population had increased to more than 200 individuals. Such changes in demographics was a result of several factors including changes in the ecology of the site, a larger forest fragment due to natural regeneration, and as a result of a female biased birth rate in the early years (Strier *et al.* 2006).

By comparing two northern muriqui groups from the same forest fragment but during different study periods (Matão group in 1983-84 and Jaó group in 2003-04) there will be an advancement in the knowledge of how group size can influence the behavioural ecology of the species.

It must be reiterated that during the different study periods the two groups differed demographically and the habitat had somewhat changed through regeneration. Both factors are likely to have also influenced the behavioural ecology of the two groups from a comparative point of view, but for the purposes of this thesis they are not the primary focus.

1.1. Objectives, Hypothesis, and Predictions

The main purpose of this thesis is to compare the Jaó (88 individuals) and Matão (26 individuals) groups from a behavioural and ecological perspective. The behavioural ecology of both groups was compared using activity budgets, diurnal activity cycles, day range travel lengths, and feeding time analyses. Group size was the main variable used to compare the Matão and Jaó groups in this thesis.

Objective: Use activity budgets, diurnal activity cycles, feeding time analyses, and day range travel lengths to compare the behavioural ecology of the Matão and Jaó groups.

Hypothesis: The larger Jaó group will experience greater intragroup feeding competition than the smaller Matão group. The result of comparatively greater intragroup feeding competition for the larger Jaó group will lead to differences in their behavioural ecology when compared to that of the smaller Matão group.

Predictions:

1: The Jaó group will spend more time feeding and travelling, and less time resting than the Matão group.

2: The Jaó group will spend more time feeding on less desirable foods such as leaves and “other” food types, and relatively less time feeding on the less available fruits and flowers (and flower products) than the Matão group.

3: The Jaó group will travel farther than the Matão group (median day range travel length).

4: The Jaó group will travel farther in the dry season than they did in the wet season; unlike the smaller Matão group whom showed no interseasonal differences (Dias & Strier, 2003).

Predictions specific of differences between male and female metabolic needs due to lactation:

6: The adult females of the Jaó group will spend more time feeding and resting, and less time travelling, than the adult males of their group; as opposed to the Matão group in which no differences were observed.

7: The Jaó group's adult females will spend more time feeding on preferred foods (fruits and flowers (and flower products)) than the adult males of their group; similar to what was recorded in the Matão group (adult females devoted more time to feeding on flowers) (Strier, 1991).

1.2. Literature Review

1.2.1. Taxonomy and Morphology

The northern muriqui (*Brachyteles hypoxanthus*) (**Fig. 1**) is a species of Neotropical primate in the *Atelidae* family. Common names for the species include northern woolly spider monkey and northern muriqui in English, and muriqui-do norte in Portuguese.

Figure 1*: A northern muriqui at the Reserva Particular Patrimônio Natural-Feliciano Miguel Abdala, ©Jean P Boubli.*

The *Brachyteles* genus is placed within the *Atelidae* family, a four-genus clade including *Ateles, Lagothrix,* and *Alouatta* (Bjarnason *et al.* 2015). Of the four genera, *Brachyteles* are only sympatric with *Alouatta* (Strier, 1992). *Atelinae* is a sub-family (*Brachyteles, Ateles, Lagothrix*)*; Brachyteles* are the only genus within it that are endemic to the Atlantic Forest (Strier & Mendes, 2012). Evidence supports a *Brachyteles-Lagothrix* clade which is sister to *Ateles*, with *Alouatta* as basal (Meireles *et al.* 1999; Di Fiore *et al.* 2015; Jameson Kielsing *et al.* 2015; Bjarnason *et al.* 2015).

There has been debate within the scientific community as to whether *B. hypoxanthus* and *B. arachnoides* form one monotypic genus or not (see Villavicencio, 2016; Chaves *et al.* 2019);

but recent phylogeographic evidence suggests that they are genetically distinct from one another (Chaves *et al.* 2019). Chaves *et al.* found that the two species “differ genetically, geographically, phenotypically, ecologically, and possibly behaviourally”. With the recent evidence, we can more confidently say that the northern muriqui is one of two species within the genus *Brachyteles*.

Both species have primarily black faces and genitalia, however *B. hypoxanthus* has mottled pink and white/grey pigmentation on the face and genitalia, and the appearance of a vestigial thumb (purely black faces and no thumb present in *B. arachnoides*) (Aguirre, 1971; Strier, 1986; Lemos De Sá *et al.* 1990; Lemos De Sá & Glander, 1993; Lemos De Sá *et al.* 1993; Strier, 1999; Cunha *et al.* 2009; Talebi, 2018). There is perhaps a difference in the level of sexual dimorphism between the two species; as no significant morphological differences between sexes have been observed for *B. hypoxanthus*, however, both upper and lower canine length was recorded as longer in a male specimen over a female specimen for *B. arachnoides* (Lemos De Sá *et al.* 1990; Lemos De Sá & Glander, 1993). The data set, however, only had two *B. arachnoides* individuals, one for each sex, so the results are of limited merit. All literature shows that *B. hypoxanthus* are sexually monomorphic; both sexes being similar in body and canine size (Hill 1962; Zingeser, 1973; Strier, 1993; Lemos De Sá *et al.* 1990; Lemos De Sá & Glander, 1993). Other molecular, morphological, and behavioural differences between the two species have been recorded (see Milton, 1984; Milton, 1985; Strier, 1987a; Strier, 1991; De Moraes *et al.* 1998, Pope, 1998, Lemos de Sá *et al.* 1993; Leigh & Jungers, 1994; Chaves *et al.* 2019).

Muriquis are the largest New World primates (Aguirre, 1971), with the northern muriqui weighing 6.9 - 9.6 kg (Lemos De Sá & Glander, 1993; not including southern specimens).

However, see Peres (1994) who suggested that extant *Brachyteles* specimens may not in fact be much larger than the *Atelines* of the northern American tropics. Muriquis, as well as being heavy arboreal primates, also have a long appearance when hanging from their arms, around 5 feet long (1.5 metres) (Strier, 1999). Nishimura (1979) described the nose of the southern muriqui (morphologically similar to the northern species) as being closer in appearance to the narrow-nosed forms of *Catarrhine* primates; as opposed to the wide-nosed forms of *Platyrrhines* (the muriquis described were at Parque Zoologico de São Paulo and were said to have been captured from São Paulo State). The pelage of the northern muriqui varies and has been described as cream to golden-grey in various literature (Nishimura, 1979; Strier, 1999). Muriquis have long, prehensile tails which have a hairless ventral surface (Rosenberger & Strier, 1989). The tail operates as a fifth limb that is often used in conjunction with a hind limb(s), or with a forelimb(s) and hind limb(s) at the same time (Lurck *et al.* 2013). The prehensile tails of muriquis are strong enough to hold their body weight whilst they feed or socialise (Rosenberger & Strier, 1989; Strier, 1999; Lurck *et al.* 2013). Prehensile tails enable suspensory locomotion, permitting the rapid movement throughout the canopy when in search for scattered fruits or escaping potential dangers (Strier, 1999). Although only a vestigial thumb remains for the northern muriqui, their other fingers are long and curved, an adaptation which allows them to hook over branches, aiding suspensory locomotion (Strier, 1999). Males have very large testicles; Nishimura reported that if humans had testicles relative to that of muriquis they would be the size of soft balls (Nishimura, 1979; Rosenberger & Strier, 1989). They have been shown to be more than six times larger than the testicles of the spider monkey’s (*Ateles geoffroyi*) and over 14 times larger than that of a brown howler monkey (*Alouatta fusca*) (Lemos De Sá & Glander, 1993). Large testicles have evolved in northern muriquis due to the apparent sperm competition as a method of selection in this species (Lemos De Sá & Glander, 1993; Strier, 1999; Talebi, 2018). Females have elongated labia and clitoris, similar to those of spider monkeys (*Ateles* spp.) (Strier, 1986; Talebi, 2018).

1.2.2. Geographic Range and Population Size

Aguirre (1971) suggested that before the arrival of the Europeans at the end of the 1500s, the entire population size of muriquis was approximately 400,000 individuals. The last population census for northern muriquis was assessed in March 2019, which estimated that there are less than 1,000 individuals remaining; accompanied by a decreasing population trend (Ferraz *et al.* 2019). This led to the classification of the species as "critically endangered A2cd".

The estimated historical distribution of *Brachyteles* spp. is from Bahia in the north to Paraná in the south (Aguirre, 1971). According to Aguirre, the northern limit to the range of *B. hypoxanthus* was likely the Rio Jequiriçá basin which spills into the Baía de Todos os Santos, and comprises the forests situated on the right bank of the Rio Paraguaçu. Less is known about the southern limit to the range of *B. hypoxanthus*, with estimations of the extremities reaching Serra da Mantiqueira; a mountain range spanning the states of Minas Gerais, Rio de Janeiro, and São Paulo (Aguirre, 1971). The historical range of *B. hypoxanthus* was estimated at 216, 330 km² (~83,525 m²) (Ingberman *et al.* 2016). Typically, muriquis inhabit areas at altitudes of 200-1200m (Talebi, 2018), but have been recorded at 1823m at Itatiaia National Park (Aximoff, 2015), and at above 2000m at Caparaó National Park (Strier *et al.* 2017).

The fragmentation of the Atlantic Forest biome, accompanied by hunting, has led to severe population decline in the *Brachyteles* genus (Ferraz *et al.* 2019). Today, the two species are believed to be geographically separated in the vast majority, if not all, of their respective known localities. The two species are suggested to have diverged 2.6 million years ago with geographical boundaries potentially at the Paraíba do Sul and Grande Rivers, and the Serra da Mantiqueira and Serra do Mar mountain ranges (Chaves *et al.* 2019). It is possible that contact zones exist within some forest fragments; for example, there may still exist a hybrid zone at the Parque Nacional do Itatiaia (PNI) (Strier *et al.* 2017; Chaves *et al.* 2019).

The northern muriqui are today distributed in 15 known fragmented forest patches within the states of Minas Gerais, Espírito Santo, Bahia, and Rio de Janeiro (Rylands *et al.* 1997; Mendes *et al.* 2005; Aximoff, 2015; Stier *et al.* 2017; Ferraz *et al.* 2019). The estimated total area size for their distribution is less than 200,000 ha (Strier *et al.* 2017; Ferraz *et al.* 2019). These localities are:

- **Áreas Particulares em Santa Maria de Jetibá** in Espírito Santo (1,000 ha); population of less than 50 mature individuals (Strier *et al.* 2017).

- **PARNA Alto Cariri** in Bahia (19,220 ha); population of less than 50 mature individuals (Strier *et al.* 2017).

- **PARNA Caparaó** in Minas Gerais/Espírito Santo (32,000 ha); minimum population of 82 mature individuals (Mendes *et al.* 2005) or less than 100 (Strier *et al.* 2017).

- **PARNA Itatiaia** in Minas Gerais and Rio De Janeiro (28,086 ha); population of more than 30 (including at least 4 infants) (Aximoff, 2015; Strier *et al.* 2017).

- **Parque Estadual Alto Cariri** in Minas Gerais (6,100 ha); population of less than 50 mature individuals (Strier *et al.* 2017).

- **Parque Estadual da Serra do Brigadeiro** in Minas Gerais (15,000 ha); minimum population of 325 (Melo *et al.* 2014) or less than 100 mature individuals (Strier *et al.* 2017).

- **Parque Estadual Do Rio Doce** in Minas Gerais (36,970 ha); population of less than 100 mature individuals (Dias, 2006; Strier *et al.* 2017).

- **Peçanha** in Minas Gerais (420 ha); population of less than 50 mature individuals (Strier *et al.* 2017).

- **REBIO Augusto Ruschi** in Espírito Santo (4,700 ha); population of 10 - 14 mature individuals (Pinto *et al.* 1993; Vieira & Mendes, 2005), or less than 50 (Strier *et al.* 2017).

- **REBIO Mata Escura** in Minas Gerais (51, 000 ha); minimum population of 28 mature individuals (Melo *et al.* 2002; Melo *et al.* 2004; Melo, 2004; Strier *et al.* 2017).

- **Reserva do Ibitipoca** in Minas Gerais (32 ha); minimum population of 7 to <50 mature individuals (Moreira *et al.* 2003; Oliveira 2003; Ferraz *et al.* 2005; Strier *et al.* 2017).

- **Reserva Particular Patrimônio Natural Fazenda Loredano Aleixo** in Minas Gerais (575 ha); population of less than 50 mature individuals (Strier *et al.* 2017).

- **Reserva Particular Patrimônio Natural-Feliciano Miguel Abdala** in Minas Gerais (957 ha); population of less than 250 mature individuals (Strier *et al.* 2017).

- **REVIS Muriquis** in Minas Gerais (2,722 ha); population of less than 50 mature individuals (Strier *et al.* 2017).

- **RPPN Mata do Sossego** in Minas Gerais (180 ha); minimum population of 42 mature individuals (Tabacow & Melo, 2013).

Local extinctions of muriquis have been recorded in various localities (Ferraz *et al.* 2019), including the Biological Station of Santa Lucia, the Biological Station of St. Lawrence, the Forest Reserve of Two Mouths, and the Forest Reserve of Pedra Azul; all of which are located in Minas Gerais state (Mendes, 1991; Ferraz *et al.* 2019).

The four largest populations (RPPN-FMA, Serra do Brigadeiro State Park, Rio Doce State Park, and Santa Maria de Jetibá) have been identified as having the greatest potential for persistence (Strier & Ives, 2012; Strier *et al.* 2017). All other populations have low numbers of mature individuals, either low double digits or single digits, so their long-term viability is not secure (Chico Mendes Institute for Biodiversity Conservation, 2011; Strier *et al.* 2017; Ferraz *et al.* 2019). Even the largest population, at the RPPN-FMA, has shown increased population fluctuations in recent years (Strier *et al.* 2017).

1.2.3. Main Threats

Northern muriquis are facing extinction due to habitat loss, habitat degradation, habitat fragmentation, hunting, fire, and disease. These threats are due to anthropogenic actions and have led to a huge reduction in the entire population size of the species over the last 500+ years since the first European settlers first arrived in Brazil.

Habitat loss and hunting have historically been the main causes of population decline of the species (Ferraz *et al.* 2019). Habitat loss is due to agriculture, urbanisation, and other anthropogenic developments. The habitat of the muriquis was destroyed because in the past it was viewed purely as a source of timber, firewood, and game; in conjunction with that, the first step in “developing” an area was seen as deforestation (Pontual & Boubli, 2005). The native fauna and flora of the Atlantic Forest have been negatively impacted due to the ensuing habitat fragmentation which has transformed the land into a matrix of degraded areas, pasture, agriculture, forestry, and urban areas; much of these areas have been used for coffee, cacao, maize, sugar-cane, or cattle (Mendes *et al.* 2005; Joly *et al.* 2014; Gross, 2017; Bogoni *et al.* 2018). Habitat loss and fragmentation have numerous damaging effects towards muriquis, some examples of which include: detrimental effects on the dispersal ability of emigrating females; isolation of populations and groups which results in genetic drift and increased inbreeding; loss of biodiversity within forest fragments; lack of habitat which lowers the carrying capacity and increases food competition amongst remaining individuals; and increased access for humans which poses threats by way of hunting and disease transmission.

Hunting was a serious threat throughout the past decades (Ferraz *et al.* 2019), which has since declined but does still occur where protection has failed (Strier, 1999). Hunting can cause imbalances in group demographics if a hunter kills more females to retrieve their infants for the pet trade or when females are slower to escape if they have dependent offspring, leaving the group with a greater male:female sex ratio (Cowlishaw & Dunbar, 2000).

Population growth is slow in muriquis, so genetic loss can occur with death in events of forest fire or disease outbreaks. Forest fires are a threat to northern muriquis; sometimes they are natural but are sometimes started unnaturally by local people (Strier, 1999). Forest fires have the potential to kill entire groups of muriquis in one hit, which for isolated populations can result in local extinctions. Disease has the potential to be of huge threat to the species, recently yellow fever has presented a risk; the population at the RPPN-FMA lost nearly 10% (N = 31) of the population and the population at Sossego lost 26% (N = 9) (Strier *et al.* 2019). Strier (1999) even suggested that the Matão group may have been below carrying capacity when she first started studying them due to a disease outbreak.

1.2.4. Muriqui Social Organisation and Behavioural Traits

Northern muriquis live in multi-male multi-female, egalitarian, groups (Strier, 1990; Strier, 1993). Flexible grouping patterns are characteristic of northern muriqui populations, with both cohesive and fission-fusion grouping patterns utilised in response to demographic and ecological conditions (Strier & Mendes, 2016). Most of the time temporary fissions have been observed, however, permanent fissions have also been recorded twice (Strier *et al.* 1993; Strier *et al.* 2006). Greater cohesiveness may be possible in smaller groups, whereas fission-fusion may become more common as group size increases to enable less competitive foraging (Dias & Strier, 2003). Male philopatry female dispersal is typically observed (Strier, 1990; Strier *et al.* 1993). Wild individuals are estimated to have a lifespan of >35 years (Strier & Mendes, 2012).

Unlike most other primate species, muriquis show little intra-group aggression over food resources, feeding sites, or sexual competition; however, both sexes do partake in defending resources against opposing groups (Strier, 1986; Strier, 1993; Strier, 1999). To reduce intra-group aggression, female muriquis will feed at an increased distance to one another to minimise feeding competition, increasing their distance from even their closest companions (Strier, 1990; Strier, 1993; Strier, 1999).

In terms of affiliative social interactions, muriquis do not groom each other, however, they do embrace each other (at least two individuals hang by their tails face-to-face whilst wrapping their arms and legs around each other) (Strier, 1999). Embraces can be dyadic or polyadic, when polyadic all-male embraces occur, they tend to heighten into more intense interactions which may include assessments of each other's strength, also acting to reinforce their cohesion (Strier, 1999). Dyadic embraces are usually accompanied by soft chuckles, whilst polyadic embraces tend to be accompanied by deeper and louder "throaty gurgles, or warbles" (Strier, 1999). The vocalisations of northern muriquis have been described as similar to the neighing of horses (Aguirre, 1971; Nishimura, 1979). Neighs are the most variable vocalisation; individuals possess unique and distinct neighs which are distinguishable by other members of the group (Strier, 1999). Individuals communicate when they are visually separated when travelling using vocalisations to maintain contact (Strier, 1990). Whilst a group are dispersed, long and loud neighs are emitted, whereas when a group are closer in proximity their neighs become shorter and softer (Strier, 1999). Chirp vocalisations occur when muriquis are feeding on preferred food sources and louder chirps can be heard from the first individual who arrives at a large fruiting patch, to which other group members react to by moving towards the location of the fruit patch (Strier, 1999).

1.2.5. Male Philopatry and Puberty

Male philopatry is observed in other primate species such as chimpanzees (*Pan troglodytes sspp.*), bonobos (*Pan paniscus*), spider monkeys (*Ateles spp.*), and other *Atelines* (Swedell, 2012). Male philopatry is advantageous for males as it ensures that even if a male does not produce his own offspring, a close relative of his should pass on similar genes to the next generation (Strier, 1993). To secure this advantage, males form strong bonds with their male relatives; cooperating to prevent opposing group males encroaching into their group and mating with the females (Strier, 1993). Male philopatry in northern muriqui is especially strong, resulting in males spending more time in close proximity to each other than what has been observed in any other primate species (Strier, 1990).

Perhaps due to high paternity uncertainty resulting from male philopatry, adult male-infant social interactions are both non-aggressive and infrequent (da Oliveira Guimarães & Strier, 2001). Strier *et al.* (2011) showed that over a two year period, the most successful reproductive male in the Matão group of muriquis at the RPPN-FMA sired just 18% of the infants that lived past 2.08 years of age. The success of that individual is strikingly low when compared to other primate species such as bonobos (*P. paniscus*) (30%), chimpanzees (*P. troglodytes*) (30-67%), and mountain gorillas (*Gorilla beringei beringei*) (85%) (data from Strier *et al.* 2011). Infanticide is considered a minimal risk for northern muriquis (da Oliveira Guimarães & Strier, 2001), which the uncertainty of paternity could explain.

Males begin sexual activity between the ages of 4.10 – 8.27 years and reach sexual maturity (defined by their first complete copulation that terminates with ejaculation) between the ages of 5.21 – 8.36 years (Strier *et al.* 2011; Strier & Mendes, 2012). Studies have shown that older more experienced males complete a greater proportion of copulations than younger males, complete more copulations during copulation months than younger males, and are preferred mating partners of reproductively experienced females (Strier, 1997; Possamai *et al.* 2005; Strier *et al.* 2011). Strier *et al.* (2011) showed, however, that paternity success had no correlation with the number of completed copulations during the copulation period and that there was no age-biased paternity.

1.2.6. Female Dispersal, Puberty, and Motherhood

Females emigrate from their natal group prior to 6.5 years of age, before the onset of puberty, and they then experience a delay in the onset of normal ovarian cycling (Strier *et al.* 1993; Strier & Ziegler, 2000). Emigration, thus, comes at a cost; as immigrant females have shown to experience this delay to usual ovarian cycles until they reach their second full mating season within their new group (Strier & Ziegler, 2000). Once the onset of puberty begins, females begin a process of irregular ovarian cycles and an infertility period of which has been documented to last approximately 14.3 months (Strier & Ziegler, 2000). Strier and Ziegler (2000) conclude that once this process is over, immigrant female muriquis first give birth around 8.7 years old. However, in the rare case of philopatric females that remain in their natal group, it appears that puberty starts earlier and they first give birth more than one year prior to emigrating females (Strier *et al.* 1993; Strier & Ziegler, 2000; Martins & Strier, 2004).

Records show that muriquis concentrate births during the cool dry season months after conceiving during the previous warm wet season (Strier, 1993; Strier, 1996; Strier *et al.* 2001). The causation of this pattern is not entirely clear; seasonality of resource availability may be the answer (Strier *et al.* 2001). Muriqui gestation length is around 7.2 months (Strier & Ziegler, 1997). Between one and a half and two and a half years of age, offspring are then weaned (Strier, 1999). The median birth interval for northern muriquis is 36 months; this interval follows infants that have survived to weaning and are more than 2 years of age (Strier *et al.* 2006).

Adult females that are in a weaning period spend less time in close proximity to adult males than do adult females in post-weaning periods (Guedes *et al.* 2008). Adult males perhaps find females in their post-weaning periods more attractive, perhaps due to their resumption of sexual activity (Strier & Ziegler, 1997; Guedes *et al.* 2008). Guedes *et al.* (2008) found that weaning females spent more time in close proximity to other females with dependant offspring; which could be due to their similar activity budgets. Post-partum cycling usually continues once their offspring is at least 2 years old and takes place during the late dry season or early rainy season, experiencing 3-6 cycles before conceiving again (Strier & Ziegler, 1997). Adult females will carry their infants up to 26 months old, after which they may still assist them in crossing wide canopy gaps by using their body as a bridge when necessary (Strier, 1999; Guedes *at al.* 2008).

1.2.7. Sexual Behaviour

Due to the sexual monomorphism of this species, and the subsequent inability for males to bully females, females have choice in their sexual partners; allowing them the option of presenting themselves to preferred mates and allowing them to avoid the advances of less desirable males (Strier, 1999). Northern muriquis are promiscuous in their sexual activities and often mate indiscreetly in view of other group members and human observers alike; at times mating can last several minutes (Strier, 1999; Strier & Ziegler, 2000). Often, females will mate with multiple males within a short period of time; sometimes in quick succession (Strier, 1999). Typically, this could cause aggression in primate societies, however muriqui males show little concern and are relaxed about the mating situation, simply waiting for their turn (Strier, 1999).

As aggressive intra-group competition for mates is absent within muriqui groups, another method for reproductive success is utilised. The large testes of the male muriqui produces great quantities of ejaculate which once copulation is complete congeals into a plug to prevent competitors' sperm from entering the female's reproductive tract; often visible for several days afterwards (Strier, 1999). However, plugs are not always successful as both the female and subsequent males have been observed removing them, and sometimes consuming them, before their own mating session (Strier, 1999).

1.2.8. Activity Budgets and Diurnal Activity Cycles of Muriquis

So far, only one activity budget that focused on an entire group has been published for northern muriquis (Strier, 1987a); this focused on the Matão group at the RPPN-FMA. One other study looked at the activity budgets of individual females at different stages of reproductivity (Guedes *et al.* 2008). Further activity budget studies are of importance as the activity budget of groups can differ even when they are within the same population (Isbell & Young, 1993); differences could suggest differing ecological or demographic pressures.

As previously mentioned, there is only one study that focused on the activity budget of an entire group of northern muriquis (Strier, 1987a); which is often used to describe the species' behavioural characteristics. The activity budget of Strier (1987a) focused on the Matão group from 1983-1984 and found that they spend almost half of their daylight time resting, followed by travelling, feeding, socialising, vocalising, and “other” activities; no intermonthly variation in time spent on activities was recorded. The Matão group appeared to shift the timing of their activities, as opposed to the proportion of time spent on activities, between seasons. During the hot and wet season, the muriquis rested during the hot mid-afternoon hours; whereas, in winter they rested until the midday hours. A distinct decrease in rest and increase in feeding prior to the onset of settling down for the night was observed.

The proportion of time spent resting, travelling, and feeding did not differ between adult males and adult females. The main differences in activity budgets were shown to occur between the adults and immatures; adults devoting more time to resting, with immatures being more active. A difference in activity budgets was observed between lactating and cycling females. One lactating female was shown to allocate significantly more time to feeding than one cycling but non-reproductive female. The effects of lactation on the female activity budget could be due to increased energy/nutrient requirements but there are other possible reasons for the differences. Strier (1987a) commented that the difference in feeding time could be due to the energy or nutrient content differences in the food items consumed between the two females, and/or could be that the females had access to more or less preferred foods or feeding sites than one another. Strier went on to mention that the latter scenario was unlikely due to the lack of feeding competition she observed. Another study (Guedes *et al.* 2008) looked at the activity budgets of weaning and post-weaning females. Guedes *et al.* (2008) found no difference in the proportion of time the respective females devoted to activities. The energetic requirements may have been similar because in the weaning year females require energy for lactation, but in the post-weaning year females require energy for infant carrying; thus, both periods required similar energy consumption; just for different reasons.

1.2.9. Muriqui Home Range and Day Range Travel Length

Fruit and flowers are the preferred foods of choice for muriquis (Strier, 1991); both of which are clumped and unpredictable in their distribution. Primates tend to live in larger groups and utilise large home ranges when foraging on clumped and unpredictable food resources (Clutton-Brock & Harvey, 1977b). Northern muriquis have been documented in using home ranges in size from 168 – 406 hectares (Strier, 1987b; Dias & Strier, 2003; Lima *et al.* 2019). It has been consistently documented that the largest group within a population of northern muriquis has the largest home range size, however, variation in home range sizes of other sized groups do not always correspond (Lima *et al.* 2019). Home ranges of northern muriquis have been documented as being stable and in the past have shown high levels of overlapping (Strier, 1987b; Dias & Strier, 2003), however, it has been shown that at the RPPN-FMA overlapping of home ranges decreased as population density increased (Lima *et al.* 2019). Muriquis show high interannual fidelity in their home range (Lima *et al.* 2019), but the time that they spend in specific areas varies between months; seasonality of food resources is one explanation for this (Strier, 1987b).

The day range travel length has been recorded over time for the Matão group at the RPPN-FMA; a mean of 1283m (between 141 – 3403m daily) was observed from June 1983 – July 1984 (Strier, 1987b) and a mean of 1313m (between 200 – 2835m daily) was observed from September 1998 – July 1999 (Dias & Strier, 2003); day travel ranges did not vary between seasons in either study period. Between the two periods, the Matão group grew from 23-27 to

57-63 individuals. The day range travel length was recorded again for the Matão group from 2010-2011 (mean of 1132m; 109-117 individuals), 2011-2012 (mean of 1064m; 117-119 individuals), and 2012-2013 (mean of 1075m; 119-130 individuals) (Lima *et al.* 2019).

1.2.10. Terrestrial Habituation

Northern muriquis are arboreal primates; however, at the RPPN-FMA over a span of 23 years, the Matão group's time spent engaged in terrestrial activities increased by 20-fold (Tabacow *et al.* 2009). The Matão group were first observed terrestrially in 1982 (Valle *et al.* 1984), and then from July 1983-1984 when just 0.12% of their recorded behavioural observations were terrestrial (Strier 1986; Tabacow *et al.* 2009). The group's terrestrial activities increased to account for 0.7% of their recorded behavioural observations from August 1998-July 1999 (Dias, 2003). Between November 2004-May 2005 resting and socialising were observed terrestrially by group members; by this time the group had increased to 80 individuals (Mourthé *et al.* 2007). Finally, from August 2006-July 2007, the group's terrestrial activities increased to account for 1% of their recorded behavioural observations.

Initially, the group may have descended to the ground as an ecological response to demographic conditions (Tabacow *et al.* 2009). The reason for this could be because as group size and population density increased so did competition for arboreal food resources so vertical niche expansion possibly was an adaptation to be able to feed on fallen fruits/previously ignored foods/previously under-utilised foods, to drink, or to travel in a saturated habitat (Tabacow *et al.* 2009; Strier & Ives, 2012).

Previously, Strier (1999) documented that the Matão group's ground use was mostly travel. Strier also documented the Jaó group's terrestrial activities, which occurred mostly during the dry season to drink water; a time when there is less available water sources within the trees (Matão group also used the ground to drink but at a significantly lower rate). The Matão group are now seemingly more relaxed in terrestrial activities (including non-essential activities such as resting and socialising) (Tabacow *et al.* 2009). This may have occurred over time due to the presence of human observers whom they have become habituated to, in conjunction with their limited experience with predators. Predation has been documented at this site, the predators being: an ocelot (*Leopardus pardalis*) (Bianchi & Mendes, 2007), possibly a tayra (*Eira barbara*) (Printes *et al.* 1996), and another unidentified felid (Possamai *et al.* 2007). Feral dogs have also been documented in the Matão group's home range, and a puma (*Puma concolor*) was reported in another part of the forest; both of these infer the potential of other predators of this group (Tabacow *et al.* 2009). Despite these recordings, the actual predation rate on this group seems to have been low (Strier *et al.* 2006). The low predation rate on this group could be due to either the presence of human observers who habituate the group and the subsequent avoidance of humans by predators of the muriquis, or a decline in the local predator community (Mourthé *et al.* 2007; Tabacow *et al.* 2009).

It appears that the Matão group's terrestrial activities are now more than just an ecological response to demographic conditions; they have become a tradition (Tabacow *et al.* 2009). The group now engage in terrestrial activities even in closed canopy locations, where arboreal opportunities are available, even at times when other group members are engaged in the same activity but arboreally; including non-essential activities such as socialising and resting (Tabacow *et al.* 2009). In terms of age-sex classes, males spent relatively more of their time engaged in terrestrial behaviours, and females were more likely to spend time on the ground when in the company of males as opposed to when they were by themselves (Tabacow *et al.* 2009). Males of the Matão group spent more time in close proximity to each other than did the females, so, terrestrial experiences occurred in a highly social context and have facilitated the spread of a tradition via male-biased social bonds (Tabacow *et al.* 2009). Other factors that support the transition from an ecological response to demographic conditions to a tradition include the large proportion of group members whom participate in terrestrial activities, and the increase in occurrence and variety of terrestrial activities.

Other explanations that have been suggested for muriqui terrestrial ground use in the literature include: females dispersing the natal group across pastureland in search for a new group, avoidance of confrontation between male subgroups, and the avoidance of aggression from an adult female towards a newly immigrated adolescent female (Lemos De Sá, 1988; Strier, 1999).

1.2.11. Evolutionary Adaptations for Diet

Within the *Atelidae* family, the most folivorous are *Alouatta* followed by *Brachyteles*; with *Lagothrix* and *Ateles* the least. Frugivory is greater in *Ateles* and *Lagothrix,* followed by *Brachyteles* and then *Alouatta* (Rosenberger & Strier, 1989; Strier, 1992; Schoeninger *et al.* 1997). Due to the larger body size of *Brachyteles* than *Alouatta*, folivory is expected to represent a greater proportion of the diet based on body size energetics (Gaulin, 1979); however, this is not the case (Strier, 1991). *Brachyteles* are closer aligned to *Alouatta* in terms of folivory than the other *Atelids* (Strier, 1992).

Adaptations to a more folivorous diet are likely to have evolved **after** adaptions for frugivory; once the species evolved in the drier, more seasonal, and more isolated Atlantic

Forest (Rosenberger, 1992; Strier, 1993). An increase in body size may have been an adaptation to a lower quality food supply (Clutton-Brock & Harvey, 1977b) in the Atlantic forest when contrasted to that of their Amazonian ancestors. Adaptations to folivory include their well-developed mandibles, chewing muscles, and sharp crested molars; which enable muriquis to chew through the cell walls of leaves and digest the nutrients more effectively (Strier, 1993). Relatively long intestines, giving muriquis a pregnant looking protruding stomach, are another evolutionary adaptation to folivory. Howler monkeys (*Alouatta* spp.) also have long intestines, however, food passes through the digestive system much quicker in muriquis (known to excrete faces every few hours) (Strier, 1993). Strier (1993) explains how the slow digestive process observed in howler monkeys allows for the digestion of leaves and acquisition of their nutrients; which due to the rapid defecation process of muriquis, reduces this ability. The rapid excretion ability of muriquis allows for a reduction in the absorption of plant tannins and toxins, as they are removed from the body very quickly. This allows muriquis to be less selective than *Alouatta* when it comes to foraging on leaves (Strier, 1993).

Northern muriquis travel via suspensory locomotion (Strier, 1993), which enables rapid movement throughout the forest, an evolutionary adaption to an ancestral diet of rich, ripe fruit (Strier, 1987b; Rosenberger & Strier, 1989). Suspensory locomotion may be the determining adaptation that allows for a lesser proportion of folivory in comparison to howlers due to the ability to monitor a greater food resource area and exploit rarer food items more frequently (Strier, 1987b; Strier, 1992). Suspensory locomotion allows for longer day travel ranges than what quadrupedal locomotion can; which permits the monitoring and exploitation of preferred food resources whilst remaining in relatively large groups (Strier, 1987b). Fission-fusion grouping is utilised to reduce feeding competition; Fissioning when fruit patches are small and fusing when large patches are available (Strier, 1992).

1.2.12. Dietary Items

Some examples of plant species that are known food sources of *B. hypoxanthus* are: *Apuleia leiocarpa, Enterolobium contortisiliquum, Euterpe edulis, Genipa americana, Hymenaea stilbocarpum, Inga* spp*, Mabea fistulifera* (Euphorbiaceae), *Palicourea tetrapylla, Platypodium elegans, Psychotria warmingii* (Rubiaceae), and *Spondias dulci* (Anacardiaceae); figs and mangoes are also a favoured food source (Aguirre, 1971; Nishimura, 1979; Hatton *et al.* 1984; Strier, 1987b; Strier, 1991; Ferrari & Strier, 1992; Strier, 1993; Mourthé *et al.* 2007; Mourthé *et al*. 2008). Strier (1991) has listed sixty three plant species, of 57 genera, that were recorded as food resources of *B. hypoxanthus*.

1.2.13. Feeding Time Analyses

Like the activity budgets of northern muriquis, there is only one feeding time analysis study of an entire group (Strier, 1991). Ferrari and Strier (1992) contributes to the literature by presenting data on feeding behaviour during nectar feeding events.

Strier (1991) provides feeding time analyses of the Matão group of 1983-1984. The Matão group devoted over half of their annual feeding time to leaves, followed by fruits, then flowers and flower products; other food items account for less than 7% of their total feeding time. Although the muriquis devoted over half of their observed feeding time to leaves, they preferred to feed on fruits and flowers when the chance presented itself (Strier, 1991; Strier, 1993). Muriquis may “camp out” in a specific area of the forest for consecutive days where particular tree species are producing ripe fruits or flowers (Strier, 1987b; Strier, 1993).

Leaves formed the majority of the Matão muriquis' diet; with immature leaves more preferable over mature leaves (Strier, 1991; Strier, 1993). Strier (1991) suggested that leaves are consumed for protein and/or to provide bulk to their diet, whilst also providing essential amino acids which are lacking in fruits (Strier, 1999). The large body size of this species results in their metabolism being relatively low; meaning they can subsist on low energy leaves for extended periods (Strier, 1999). Despite the amount of time spent feeding on leaves overall, they are most commonly foraged upon during the search for fruits; only receiving more attention when fruit is scarce (Strier, 1993). At the RPPN-FMA, during late September-mid October, muriquis are observed camping out like they do for preferred fruits and flowers, although during this time it is to forage on the leaves of two tree species (*Apuleia leiocarpa* and *Platypodium elegans*); both are species in the legume family and appear to be valued during times of fruit scarcity (Strier, 1993).

When feeding on flowers, muriquis usually eat the entirety of the mature flower, however, when it comes to *Mabea* the nectar and pollen are eaten exclusively (Strier, 1991; Strier, 1999). Ferrari and Strier (1992) provide feeding behavioural data of nectar feeding events and described these occurrences as discrete events. This was due to the fact that during 84.2% of scan samples only one individual was recorded feeding on nectar at any one time; and never more than two. There was also a lack of synchrony between group members regarding nectar feeding, and the same individual was rarely documented in successive scan samples feeding on nectar. The consumption of *M. fistulifera* nectar was greater during periods of fruit scarcity; this is another example of the flexibility of their diet and how these primates utilise their forest ecosystem.

1.2.14. Seasonal Variability in Feeding Time

The proportion of time spent feeding on different food types across sample periods during Strier's (1991) study of the Matão group was shown to be highly variable; for example, muriquis adapted and were more folivorous when fruits became scarce (Strier, 1991; Ferrari & Strier, 1992). The variation in their diet was likely caused by seasonal differences in rainfall and food resource availability (Strier, 1993); also observed in other primates (Isbell & Young, 1993).

Muriquis have particular food sources with which they seek out during certain times of the year. *Enterolobium contortisiliquum* is the fruit of a legume species that the muriquis feed on sparingly in the dry season; leaving their usual central forest range for the periphery where these fruits are found (Strier, 1993). Strier reported (1993) that the muriquis only briefly feed on these fruits before moving on, whereas other fruit sources are foraged on until depletion.

1.2.15. Sex Differences in Feeding Time

Males and females of the Matão group (Strier, 1991) did not differ in the proportion of time they devoted to feeding on fruits and leaves; however, adult females were shown to devote more time to feeding on flowers than the adult males did. During Strier's study, only one of the eight females were lactating, Strier added that if this number was greater, then perhaps there would have been greater differences between the sexes. So, the diets of the male and female seemingly resemble one another when removed of the added metabolic stress of lactation (Strier, 1991). Strier proposed an alternative reason for the resembling diets; due to the population being below carrying capacity at the time, feeding competition for preferred fruit resources was reduced, enabling males to consume a similar diet to that of the females.

1.2.16. Seed Consumption and Dispersal

Muriquis are known to be seasonal seed predators of *M. fistulifera*; consuming the seeds when the fruits are at an early stage of ripeness (Mourthé *et al.* 2008). Mourthé *et al.* provides evidence that puncture resistance is the method of selecting seeds of *M. fistulifera* for consumption; due to the lack of specialised anatomical adaptations in *Brachyteles* spp. for the exploitation of hard fruits.

Though they are seed predators of *M. fistulifera*, northern muriquis are also important seed and pollen dispersers for the ecological health of the Atlantic Forest. Observations of the muriquis foraging on the nectar of *M. fistulifera* revealed how pollen was often visibly covering the face and hands of the individuals afterwards (Ferrari & Strier, 1992). Pollination follows when the monkeys move on to other trees and resume foraging.

1.2.17. The Importance of Conserving Muriquis

Keystone Species: Northern muriquis significantly alter their environment with their seed dispersal ability which leads to a more biodiverse habitat. This species is of even greater importance in forest fragments which have experienced the extirpation of other large frugivores that would have contributed to seed dispersal.

Umbrella Species: The conservation of the northern muriqui also indirectly acts as conservation of the Atlantic Forest ecosystem. Protecting forest fragments which muriquis inhabit will also serve as protection of other fauna and flora. Protection of the northern muriqui would provide protection to species such as: the buff-headed capuchin (*Sapajus xanthosternos*) (Critically Endangered), buffy-headed marmoset (*Callithrix flaviceps*) (Endangered), buffy-tufted ear marmoset (*C. aurita*) (Endangered), crested capuchin (*S. robustus*) (Endangered), giant armadillo (*Priodontes maximus*) (Vulnerable), and the maned three-toed sloth (*Bradypus torquatus*) (Vulnerable) (International Union for Conservation of Nature, 2020).

The conservation of this species has a wide spreading impact on the surrounding fauna and flora of the Atlantic Forest and for that reason alone their conservation is invaluable. Northern muriquis, though, are important also for primatological studies as the ecological pressures that this species face and their ensuing behavioural, societal, and dietary adaptations are quite unique. There is still so much to be learnt through the monitoring and research of this species.

1.2.18. Further Research Required

The vast majority of behavioural and dietary studies on northern muriquis have been conducted at the RPPN-FMA by Dr Karen Strier and collaborating researchers. Data from other populations at other sites could provide new insights into the behaviour and diet of this species when faced with differing ecological pressures. Strier *et al.* (2017) lists the other known localities of muriqui populations and provides a scale rating of the implementability of field research; as well as the size and genetic uniqueness of each population. Research into the other populations would be highly beneficial in adding to the current literature on the northern muriqui.

2. Methods

All data were collected by Jean Boubli, Ítalo Mourthé, and Marcos Tokuda. The methods they used to collect the data will be stated under the headings **2.3.** and **2.4.**; the methods I used to analyse the data are presented under the heading **2.5.**

2.1. Study Site

The study was conducted at the RPPN-FMA, part of the Rio Doce basin; approximately 300km north of Rio de Janeiro and 52km east of a town named Caratinga, at 19° 50’S 41° 50’W (Strier, 1986; Boubli *et al.* 2011) (**Fig. 2**). The forest is privately owned, and approximately 1,000 hectares, and is located on Fazenda Montes Claros, Minas Gerais, Brazil. The forest is a fragment of the once vast and connected Atlantic Forest, which now finds itself surrounded by pasture and crop land, primarily coffee (Pontual & Boubli, 2005).

Three main drainage systems (valleys) are present at the RPPN-FMA; Matão, Jaó, and Sapo. The location of this study was the Jaó valley (~490ha); which is located in the northern side of the forest (Boubli *et al.* 2011).

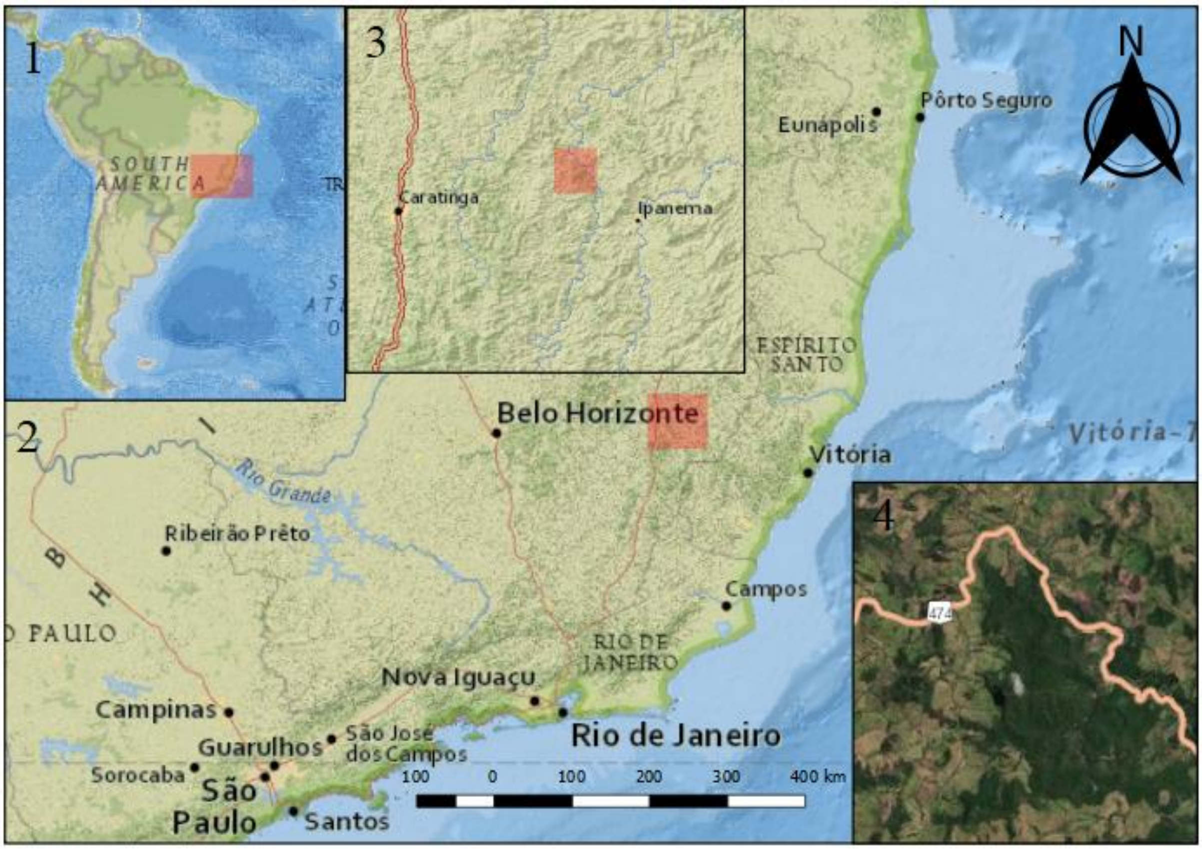

Figure 2*: The location of the RPPN-FMA in relation to 1) South America, 2) South-Eastern Brazil, 3) The State of Minas Gerais, 4) The immediate vicinity of the surrounding area. This map was created using QGIS version 2.18 using the QuickMapServices plugin; specifically, ESRI maps; including ESRI National Geographic and ESRI Satellite.*

The climate of the Atlantic Forest is classified as "Tropical Atlantic Morphoclimatic Domain" (Ab'Saber, 1977). The habitat at the RPPN-FMA experiences high seasonal changes regarding rainfall and the availability of preferred muriqui food sources; both of which influence the behaviour, ecology, and reproduction of the muriquis at this site (Strier 1986; Strier & Ziegler, 1997). The altitude ranges from 318m to 628m (Pereira *et al.* 2010) and is made up of a series of hills and valleys. Hilltop vegetation varies in both forest structure and plant species composition when compared to the vegetation of the valleys (Boubli *et al.* 2011).

2.1.1. Disturbances at this Site

As is typical of remaining Atlantic Forest fragments, this site has many signs which point to a long history of selective logging, including a discontinuous top canopy layer and few large emergent trees (Boubli *et al.* 2011). The ecosystem of a disturbed forest has been disrupted in its nature, resulting in local extinctions of some species, whilst increasing the success of other species and thus, a shift in species composition.

The disturbance at the RPPN-FMA has resulted in a mosaic of forest of differing regenerative stages (Strier & Boubli, 2006). Another issue that has been created by high disturbance is greater liana growth. Dense liana infestation has presented a problem for forest regeneration at this site; >52% of trees sampled there had at least one liana obstructing their crown (Boubli *et al.* 2011). In some hilltop areas bracken has covered the forest floor; leading to gaps in the canopy of more than 20 metres in diameter (Boubli *et al.* 2011). These gaps in the canopy present a problem for arboreal species such as muriquis, which may compel individuals to travel terrestrially, which would pose a threat to their safety due to predation by terrestrial predators (domestic dogs, large cats).

2.2. Study Group

This thesis uses data from the Jaó group which was collected between March 2003-March 2004. The Jaó group has been systematically studied since June 2002, although opportunistic data has been recorded since 1983 (Strier *et al*. 2006).

The demographics of the Jaó group during the study period consisted of a total of 88 individuals. The age and sex classes consisted of 41 males (25 adults, 3 sub-adults, 10 juveniles, 3 infants) and 47 females (31 adults, 6 sub-adults, 5 juveniles, 5 infants).

2.3. Habituation of the Jaó Group

The first stage of the study was the habituation process of the muriquis at the RPPN-FMA. Trails were opened within the home range of the Jaó group to facilitate the search effort and to ease the tracking of the muriquis.

2.4. Behavioural Sampling

Once the habituation process was complete, the muriquis were followed from dawn to dusk for 5-17 days per month (an average of 13.1 days per month). This cumulated in the acquisition of data covering 170 days over the total sample period, which began on the 3rd March 2003 and ended with data collected on 18th March 2004.

Of the 170 sample days; males were present for 168 of the days; females were present for 156 of the days; and both sexes were present for 154 of the days; these totals are not mutually exclusive from one another.

All of the methodology used for behavioural data collection in this study follows methods implemented by Strier (1986; 1987a). For comparative purposes, activity budget data was collected following Strier (1987a); instantaneous scan samples (Altmann, 1974) were taken for 5 minutes at 15 minute intervals to estimate the activity budget of the group. During scan samples each monkey was identified, if possible, by their facial markings and their activities were recorded. If an individual could not be identified then, if possible, their age-sex class was recorded. The following activities were recorded: **1.)** *rest,* **2.)** *travel,* **3.)** *feed,* **4.)** *social,* **5.)** *vocal,* **6.)** *other.* For definitions of each category, see Strier (1987a). Also, during every scan sample a GPS coordinate was taken, this was used to calculate the day range travel length of the Jaó group.

For the feeding time analyses, feeding data was collected whenever feeding behaviour was observed using certain parameters to identify the specific food type. The parameters were as followed: **1.)** food type: *a) fruit, b) leaves, c) flowers, d) buds, e) stems, f) bamboo, g) nectar, h) bark, i) undetermined.* **2.)** stage of ripeness: *a) mature, b) immature.*

Food type was listed as undetermined when the food item could not be identified. Stems, bamboo, and bark were sometimes combined as a group named as “Other”. Flower and flower products (nectar and buds) were sometimes combined as a group named as “Flower*”. When the stage of ripeness could not be determined then a group named as either “Fruit of Unknown Maturity” or “Leaf of Unknown Maturity” was used.

2.5. Data Analyses

To reduce potential biases well known in this sampling technique (Altmann, 1974; Clutton-Brock, 1977), each individual scan sample was treated as a single observation; following the methods used by Strier (1987a). With our data analyses I divided the samples into the months of the year, of which 13 were covered. I did not divide the sample days to correspond to the schedule of phenological sampling as did Strier (1986; 1987a; 1991).

Using Microsoft Excel’s pivot table function, an estimation of the proportion of time that the monkeys spent on each of the six activities during each scan sample was calculated. With the averages of each scan sample calculated, daily, monthly, and the overall proportion of time that the monkeys devoted to each of the six activities were calculated.

The diurnal activity cycles were estimated using the average proportion of time devoted to each of the six activities in hourly classes from 0500h to 1800h following Strier (1987a). The overall diurnal activity cycle was calculated over 170 sample days. The wet season included data from March 2003, and November-March 2004 (72 days). The dry season included data from May-September 2003 (68 days), there were no observations during the dry season during 0500-0559h so data started at 0600h.

Age and sex classes were recorded during data collection, and so we separated the data set into their respective groups before using the same approach as described for the overall and monthly activity budgets to get the activity budgets of different age-sex classes.

The GPS coordinates that were taken were placed on a map to calculate the muriquis' day range travel length. Minitab 18 was used to calculate the average day range travel length by using data from 144 days. 59 days during March 2003, and November 2003-March 2004 were used to calculate the average day range travel length of the wet season. 60 days during May-September 2003 were used to calculate the average day range travel length of the dry season. The maximum, minimum, and median day range travel length of each time period were also calculated. A Two-Sample t-Test was used to test the difference between the day range travel lengths of the wet and dry seasons.

Feeding time was calculated following the same method as used to calculate the activity budgets, however, the activity variable was replaced by the food type variable. Age-sex class differences in feeding time was calculated as stated for age-sex class differences in activity budgets; by separating the data into groups and then following the method for calculating the overall feeding time.

Between my discussion and results sections, the first thing to state is that there are some differences in the feeding time analyses data, which will be listed alongside the reasoning:

- The means for the Jaó group's "Flower*" in my discussion (**Table X** and **Table XI)** differ from those in my results section (**Table V**) due to the fact that in the results section I grouped flowers, nectar, and buds as Flower*, whereas in the discussion section in order to compare to Strier (1991) I grouped only flowers and nectar as Flower*.

- The means for the Jaó group's "Other*" in my discussion (**Table X** and **Table XI**) differ from those in my results section (**Table V**) due to the fact that in:

  a) the results section: "Other" includes stems, bamboo, and bark;

  b) discussion **Table X**: "Other*" includes bamboo, bark, buds, stems, and undetermined food items;

  c) discussion **Table XI**: "Other*" includes buds, stems, and undetermined food items.

The reason for the changes of grouping from my results to my discussion was to be more comparable to Strier (1991).

- The Matão group's "Other*" is different in my thesis (**Table X** and **Table XI**) than in Strier's (1991) paper due to the fact that we **did not** collect data for "Seeds" and so I grouped her "Seeds" mean with her "Other" mean total.

- The Matão group’s “Other*” also differs in my discussion between **Table X** and **Table XI** due to the fact that in:

  a) **Table X**: “Other*” includes bamboo, bark, seeds, buds, and ferns

  b) **Table XI**: “Other*” includes seeds, buds and ferns.

For any future publications I would make the necessary changes to the grouping of the Jaó group’s food types to better resemble Strier’s (1991) paper in my results section to minimise the confusion which this may potentially cause.

In summary, in the results section I categorised the food types which I then altered slightly in the discussion when comparing with the Matão group (Strier, 1991) to provide a better comparison.

All data analyses were performed in either Microsoft Excel or Minitab 18.

3. Results

3.1. Overall Activity Budget and Intermonthly Variation

The Jaó group spent a monthly average of 43.31% of their time resting, 27.37% travelling, 21.79% feeding, 6.38% socialising, 0.34% vocalising, and 0.81% engaged in other activities (**Table I**; **Fig. 3**).

The time devoted to each activity varied significantly across sample periods for all activities (**rest** *p* value 0.00, **travel** *p* value 0.00, **feed** *p* value 0.00, **social** *p* value 0.00, **other** *p* value 0.03) except from **vocal** (*p* value 0.07) (ANOVA General Linear Model) (see **Appendix I**). Tukey pairwise comparisons of the sample periods can be found in **Appendix II** which shows where the significant differences were over the sample periods.

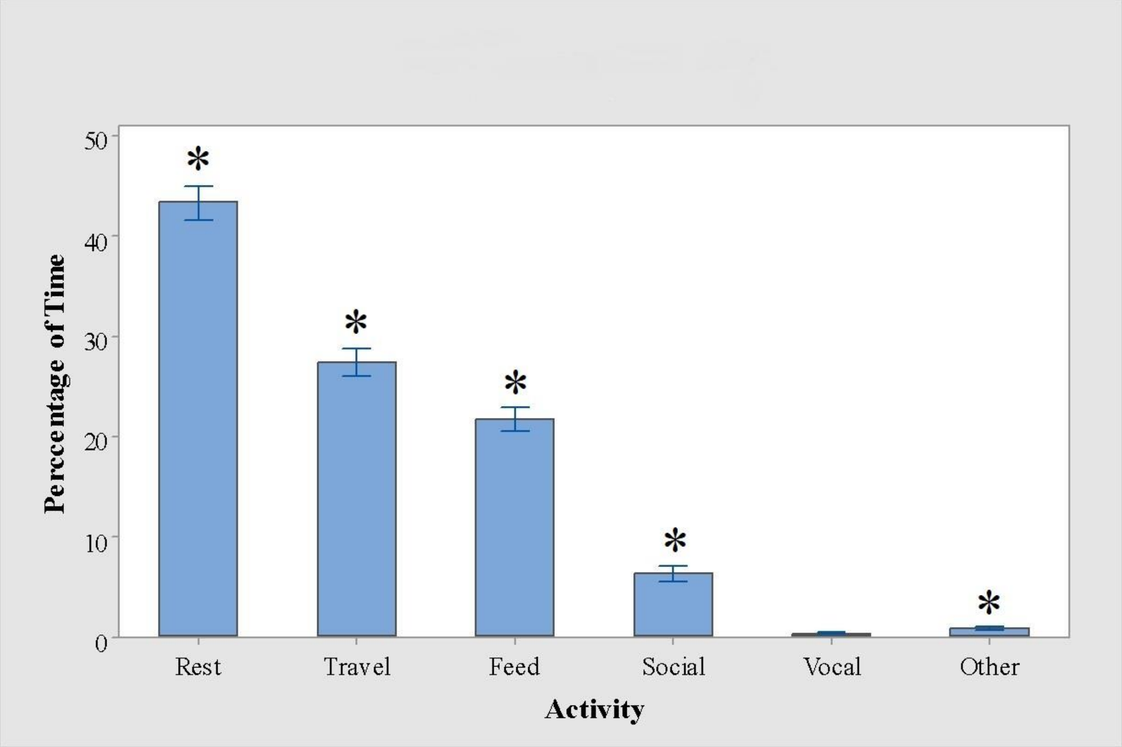

Figure 3*: The activity budget of the Jaó group. 95% confidence interval for the mean. Asterisks show that the time spent devoted to an activity varied significantly across sample periods.*

***Table I**: The overall and intermonthly variation of time devoted to each activity over sample periods in percentage.*

Sample Period	Rest	Travel	Feed	Social	Vocal	Other
Mar-03	37.83	34.4	14.87	11.28	0.24	1.37
Apr-03	39.23	31.43	16.51	12.09	0.38	0.34
May-03	42.82	28.93	16.25	10.88	0.58	0.54
Jun-03	46.46	25.05	24.37	3.35	0.44	0.33
Jul-03	36.43	32.75	26.34	3.65	0.2	0.63
Aug-03	39.76	37.41	21.13	1	0.01	0.69
Sep-03	50.06	21.54	24.58	3.32	0	0.51
Oct-03	47.38	21.99	22.31	7.46	0.26	0.61
Nov-03	43.05	25.58	22.26	6.39	1	1.72
Dec-03	49.38	25.49	20.92	3.38	0.37	0.47
Jan-04	46.14	23.37	22.53	6.08	0.35	1.52
Feb-04	46.54	22.59	24.85	4.61	0.53	0.89
Mar-04	44.57	21.77	27.06	5.7	0.32	0.58
Mean	43.31	27.37	21.79	6.38	0.34	0.81
StDev	18.12	15.44	12.52	8.78	1.14	2.07
Variance	328.35	238.45	156.73	77.02	1.31	4.27
Median	43.75	25	20.25	2.7	0	0

3.2. Diurnal Activity Cycles

The average overall diurnal activity cycle, based on 170 sample days, shows a distinct peak in rest during the late morning-mid-afternoon hours. A peak in feeding prior to the onset of resting for the night was typical, with a spike in travel time in the hour preceding. Social activity typically increased during periods of rest, especially during the midday/mid-afternoon resting period; as well as during the last hour of observations (**Fig. 4**).

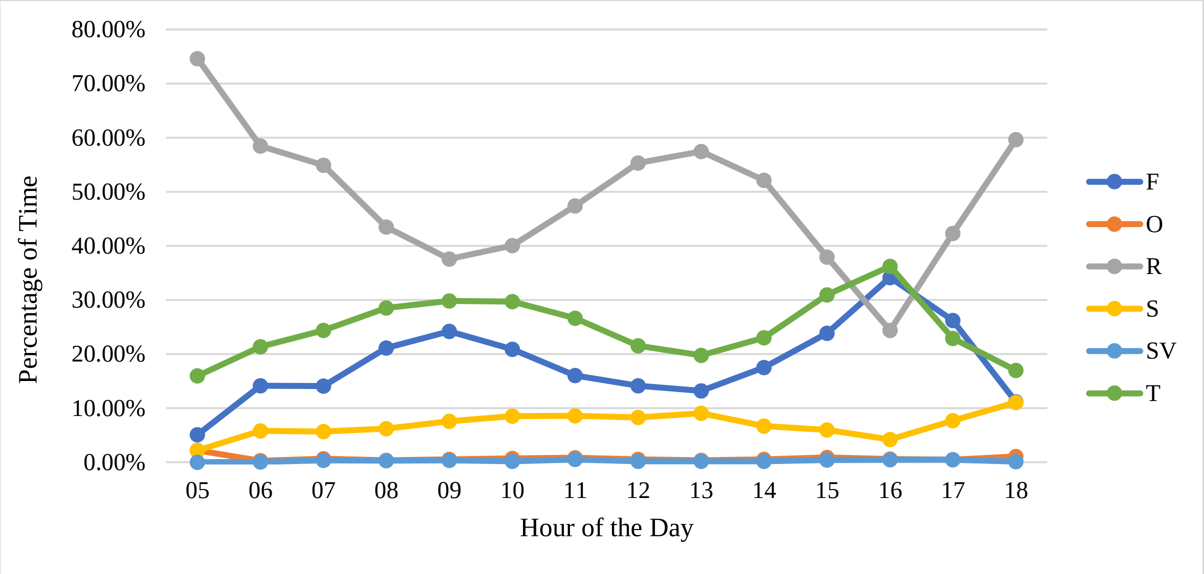

***Figure 4**: The diurnal activity cycle of the Jaó group. F = Feed, O = Other, R = Rest, S = Social, SV = Vocal, T = Travel.*

3.2.1. Wet Season Diurnal Activity Cycle

The Jaó group's wet season diurnal activity cycle, based on 72 days, was similar to their overall diurnal activity cycle. An increase in travel and feeding, coincided by a decline in rest, was typical between 08:00-08:59. The monkeys rested more during the late morning to mid-afternoon hours. A peak in feeding behaviour occurred in the late afternoon prior to the onset of settling down for the night. Social behaviour appears to have increased when resting did (**Fig. 5**).

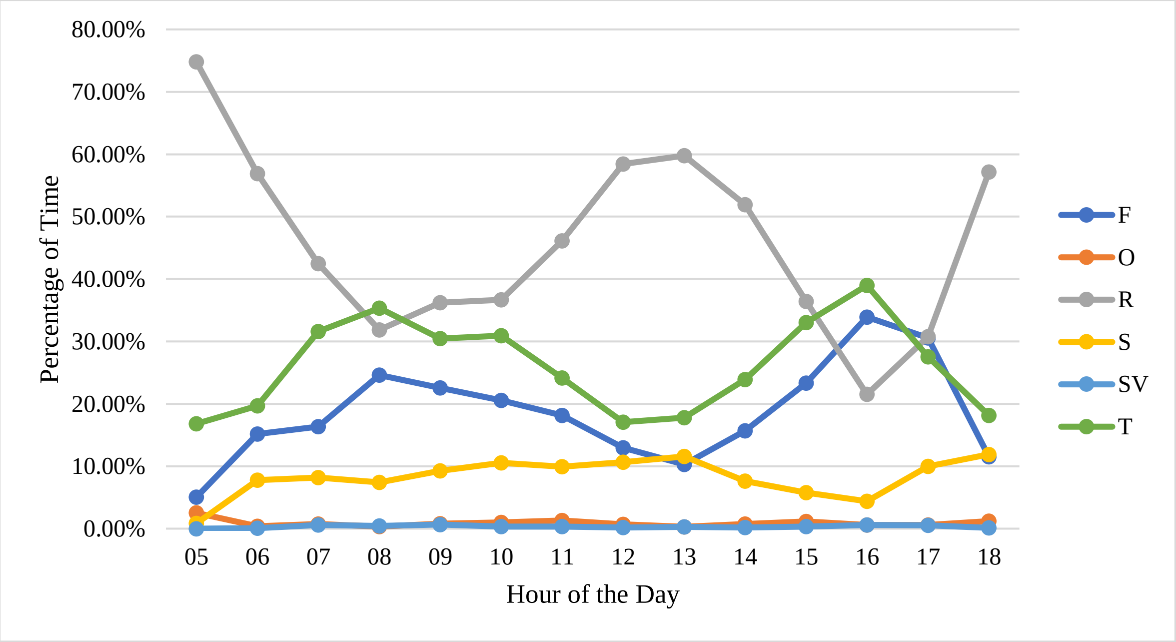

Figure 5*: The wet season diurnal activity cycle of the Jaó group. F = Feed, O = Other, R = Rest, S = Social, SV = Vocal, T = Travel.*

3.2.2. Dry Season Diurnal Activity Cycle

The Jaó group's dry season diurnal activity cycle, based on 68 sample days, shows that they were less active in the mornings, spending a greater proportion of their time resting. From 09:00 until 10:59 there was a spike in travel and feeding behaviour, accompanied by a decline in rest. The group would then rest again from midday to mid-afternoon. There was a distinct increase in travel and feeding in the late afternoon, coinciding with a decline in rest. Social behaviour was observed to a lesser extent during the dry season and did not vary greatly between hourly periods (**Fig. 6**).

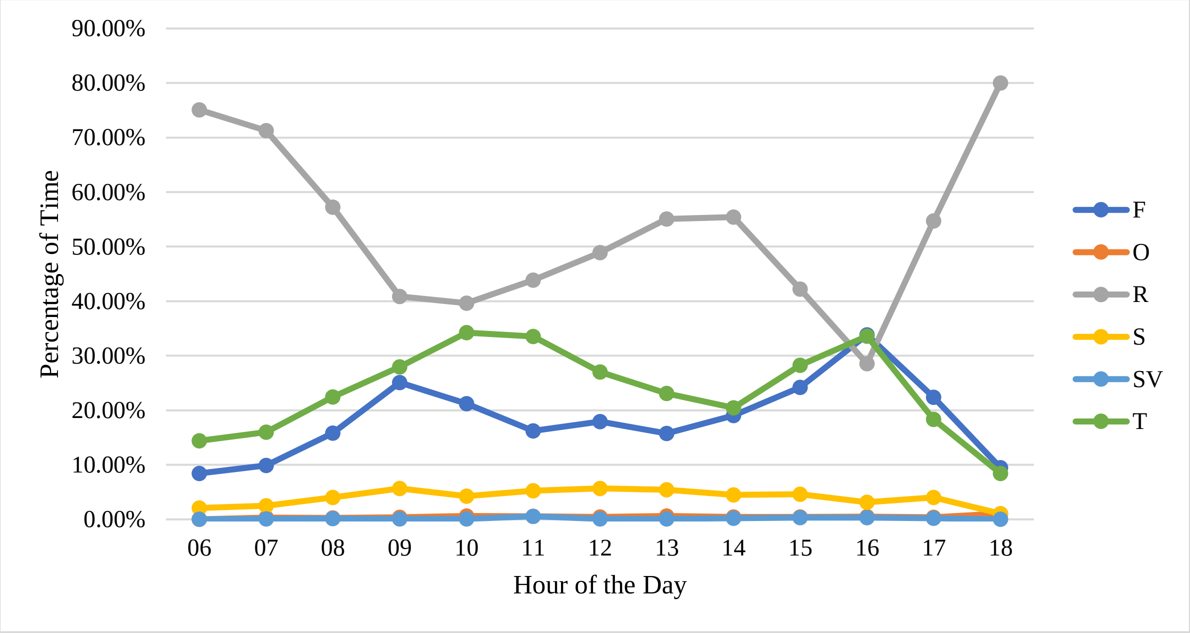

Figure 6*: The dry season diurnal cycle of the Jaó group. F = Feed, O = Other, R = Rest, S = Social, SV = Vocal, T = Travel.*

3.3. Age-Sex Class Variation in Activity Budgets

The age-sex classes were categorised as 1) adult females, 2) adult males, and 3) immature individuals. For this thesis, immature individuals included: infants, juveniles, and sub-adults; this was a mixed sexed group. Age-sex class categorisations can be found in the supplementary material of Strier *et al*. (2017). In Strier *et al.* (2017) infants, juveniles, and sub-adults are categorically different from one another by definition.

In total, there were 170 sample days; during 168 of these days males were recorded; 156 of these days females were recorded; and 160 of these days immature individuals were recorded. These totals are not mutually exclusive of one another.

When the Jaó group were analysed as three distinct subsets of groups there was a significant difference between the time they devoted to each activity (**rest** *p* value 0.00, **travel** *p* value 0.00, **feed** *p* value 0.00, **social** *p* value 0.00, **vocal** *p* value 0.01, **other** *p* value 0.00) (ANOVA General Linear Model) (see **Appendix III**; **Fig. 7**). However, sometimes this was due to just **one of the subsets** that devoted a significantly different amount of time towards an activity than the other two (**Table II**). A summary of these are that immature individuals devoted the least amount of time to resting, adult females devoted the most amount of time to feeding, adult males devoted the least amount of time vocalising, and adult females devoted the most amount of time to other activities.

Tukey pairwise comparisons of the time each subset spent on activities can be found in **Appendix IV** which shows where the significant differences were between subsets.

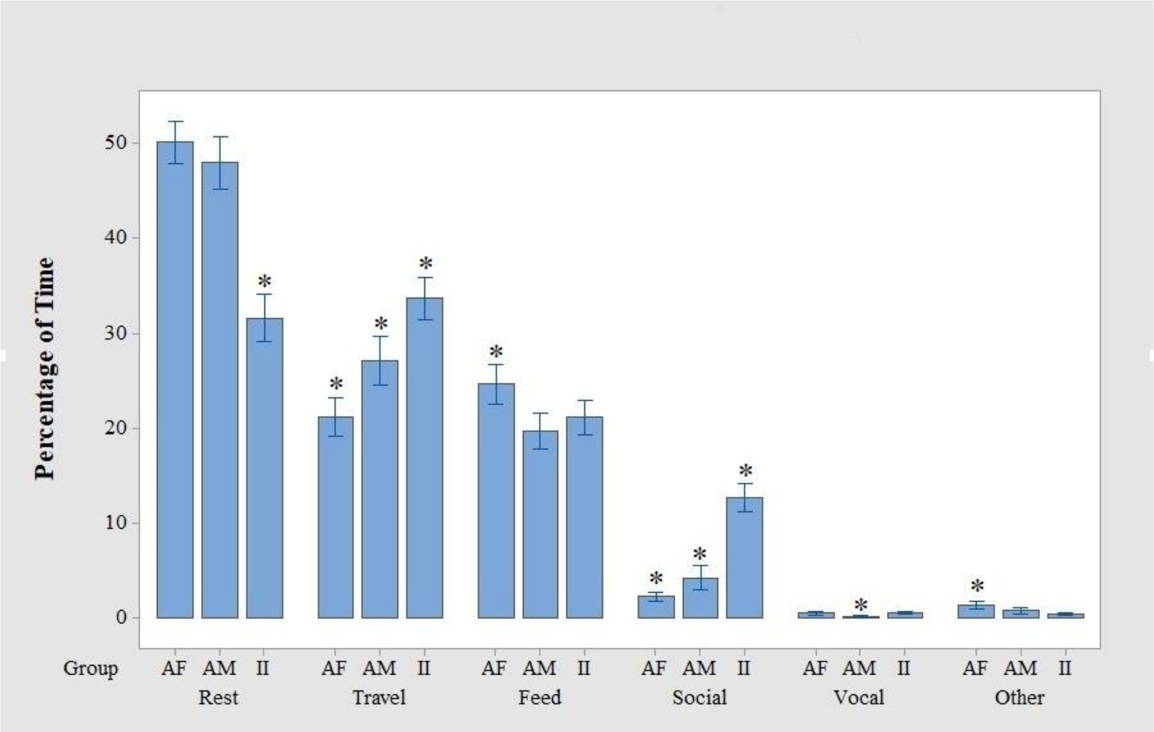

***Figure 7**: Age-sex class variation in activity budgets. 95% confidence interval for the mean. AF = adult females, AM = adult males, II = immature individuals. Significant differences between age-sex classes marked with an asterisk.*

***Table II**: The proportion of time (%) devoted to each activity over the entire sample period for each of the three groups. Sorted by means in descending order.*

Activity	Group	Mean	StDev	Variance	Median
Rest	Adult Female	50.17	14.24	202.68	52.22
	Adult Male	48.04	18.18	330.34	50.00
	Immature Individual	31.65	15.76	248.35	30.00
Travel	Adult Female	21.16	12.94	167.41	18.96
	Adult Male	27.13	16.45	270.70	24.95
	Immature Individual	33.69	14.15	200.18	33.33
Feed	Adult Female	24.63	13.09	171.37	23.45
	Adult Male	19.76	12.43	154.44	18.05
	Immature Individual	21.14	11.62	135.10	19.71
Social	Adult Female	2.23	2.96	8.74	1.27
	Adult Male	4.21	8.22	67.62	0.17
	Immature Individual	12.72	9.62	92.53	11.11
Vocal	Adult Female	0.46	1.39	1.92	0.00
	Adult Male	0.10	1.03	1.06	0.00
	Immature Individual	0.47	0.95	0.91	0.00
Other	Adult Female	1.36	2.52	6.36	0.78
	Adult Male	0.76	2.30	5.27	0.00
	Immature Individual	0.32	0.85	0.73	0.00

3.4. Correlations Between Activities and/or Foraging Patterns

Pearson correlation tests were used to test for correlations between the time the Jaó group spent engaged in different activities and/or engaged in feeding on different food types.

***Table III**: Correlation between Rest, Travel, Feed, Fruit, Leaf, Flower*. Cell Contents: Pearson correlation (above), p Value (below). Significant Results are in bold.*

Variable	Rest	Travel	Feed	Fruit	Leaf
Travel	**-0.851** >**0.001**				
Feed	0.366 0.218	-0.53 0.062			
Fruit	-0.16 0.601	0.288 0.34	-0.388 0.19		
Leaf	0.245 0.419	-0.268 0.377	**0.756** **0.003**	**-0.59** **0.034**	
Flower*	-0.123 0.689	-0.026 0.932	-0.322 0.283	**-0.652** **0.016**	-0.192 0.53

Table IV*: Correlation between Rest, Travel, Feed, Mature Fruit (MtFr), Immature Fruit (ImFr), Mature Leaf (MtLv), Immature Leaf (ImLv), Flower (Flow), Bud, and Nectar (Nect). Cell Contents: Pearson correlation (above), p Value (below). Significant Results are in Bold.*

Variable	Rest	Travel	Feed	MtFr	ImFr	MtLv	ImLv	Flow	Bud
Travel	**-0.851** >**0.001**								
Feed	0.366 0.218	-0.53 0.062							
MtFr	-0.388 0.19	0.522 0.067	**-0.736** **0.004**						
ImFr	0.282 0.351	-0.29 0.337	0.423 0.149	-0.51 0.075					
MtLv	-0.41 0.164	0.406 0.169	0.302 0.316	-0.093 0.762	-0.005 0.986				
ImLv	**0.559** **0.047**	**-0.569** **0.043**	0.155 0.613	-0.389 0.189	0.172 0.575	**-0.819** **0.001**			
Flow	-0.117 0.703	-0.043 0.889	-0.051 0.869	-0.131 0.671	-0.499 0.083	-0.184 0.547	0.162 0.598		
Bud	0.392 0.185	-0.444 0.129	0.121 0.693	-0.018 0.954	**-0.625** **0.022**	-0.105 0.734	0.22 0.47	0.342 0.252	
Nect	-0.322 0.283	0.273 0.367	**-0.58** **0.038**	0.235 0.44	-0.365 0.22	0.109 0.724	-0.327 0.275	-0.041 0.893	0.024 0.938

As expected there was a negative correlation between rest and travel (Pearson Correlation -0.851, *p* value >0.001, **Table III**), as they are opposing activities.

There was a positive correlation between the time devoted to overall feeding, and the time devoted to feeding on leaves (Pearson correlation 0.756, *p* value 0.003, **Table III**). Generally, the more time spent feeding on leaves meant that there was more time spent feeding overall.

A negative correlation (Pearson Correlation -0.590, *p* value 0.034, **Table III**) was observed between the time devoted to feeding on fruits and the time devoted to feeding on leaves.

A negative correlation (Pearson Correlation -0.652, *p* value 0.016, **Table III**) was observed between the time devoted to feeding on fruits and the time devoted to feeding on flowers (and flower products).

A negative correlation (Pearson Correlation -0.736, *p* value 0.004, **Table IV**) was observed between the time devoted to overall feeding and time devoted to feeding on mature fruits. The more time the Jaó group devoted to feeding on mature fruits, the less time they spent feeding overall.

A positive correlation (Pearson Correlation 0.559, *p* value 0.047, **Table IV**) was observed between the time devoted to resting and the time devoted to feeding on immature leaves. Contrariwise, a negative correlation (Pearson Correlation -0.569, *p* value 0.043, **Table IV**) was observed between the time devoted to travelling and time devoted to feeding on immature leaves. These two correlations indicate that when the Jaó group devoted more time to feeding on immature leaves, the proportion of time spent travelling decreased and the proportion of time spent resting increased.

There was a negative correlation (Pearson Correlation -0.625, *p* value 0.022, **Table IV**) between the time devoted to feeding on immature fruits and buds.

There was a negative correlation (Pearson Correlation -0.819, *p* value 0.001, **Table IV**) between the time devoted to feeding on mature leaves and the time devoted to feeding on immature leaves.

There was a negative correlation (Pearson Correlation -0.580, *p* value 0.038, **Table IV**) between the time spent devoted to overall feeding and feeding on nectar. Nectar was only recorded as a food source in April and May 2003, but during those sample periods the time spent feeding overall decreased.

3.5. Overall Diet and Intermonthly Variation

The Jaó group devoted 37.10% of their time feeding to fruits, 43.56% to leaves, 15.63% to flowers* (flowers and flower products), 1.99% to other food items, and 1.71% to food items that could not be determined (**Table V**; **Fig. 8**). Fruits, leaves, and flowers* contributed to >96% of the Jaó group's diet over the entire sample period.

A more in depth look into the diet of the Jaó group shows that they devoted more time feeding on immature fruits than mature fruits; and more time feeding on mature leaves than immature leaves (**Table VI**; **Fig. 9**).

The time devoted to almost every food type was highly variable over sample periods (**fruit** *p* value 0.00, **leaf** *p* value 0.00, **flower*** *p* value 0.00, **other** *p* value 0.00, **undetermined** *p* value 0.00) (ANOVA General Linear Model) (see **Appendix V**); (**mature fruit** *p* value 0.00, **immature fruit** *p* value 0.00, **fruit of unknown maturity** *p* value 0.00, **mature leaf** *p* value 0.00, **immature leaf** *p* value 0.00, **leaf of unknown maturity** *p* value 0.00, **flower** *p* value 0.00, **bud** *p* value 0.00, **bamboo** *p* value 0.00, **nectar** *p* value 0.00, **bark** *p* value 0.00, **undetermined** *p* value 0.00) (ANOVA General Linear Model) (see **Appendix VII**). The only food type which was not variable over sample periods was **stems** (*p* value 0.05); which only represented 0.84% of the Jaó group's diet (**Table VI**; see **Appendix VII**). Tukey pairwise comparisons of the sample periods can be found in **Appendix VI** and **Appendix VIII** which shows where the significant differences were over sample periods.

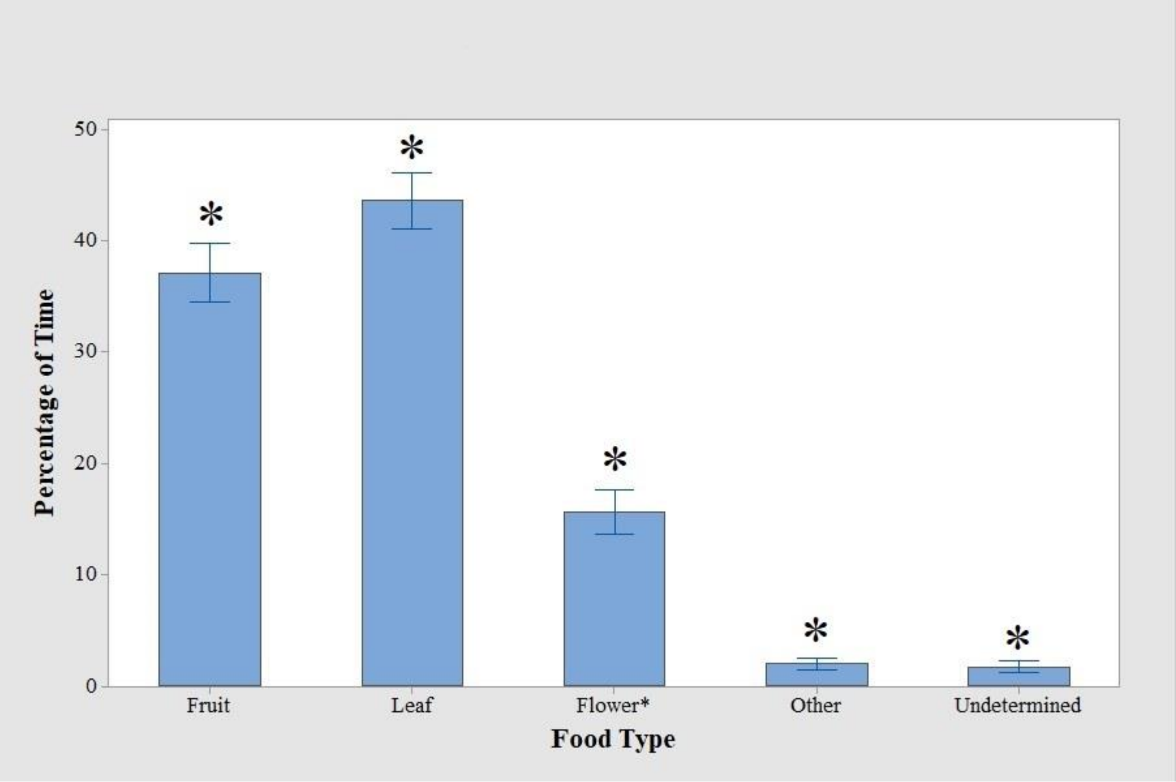

Figure 8*: Diet of the Jaó group. 95% confidence interval for the mean. Flower* = flowers and flower products. Asterisks show that the time spent devoted to feeding on a food type varied significantly across sample periods.*

Table V*: The overall and intermonthly variation of time devoted to each food type over sample periods in percentages.*

Sample Period	Fruit	Leaf	Flower*	Other	Undetermined
Mar-03	59.94	25.85	12.80	0.78	0.63
Apr-03	30.06	39.23	30.43	0.00	0.28
May-03	46.26	32.99	19.23	0.81	0.70
Jun-03	49.66	44.64	3.47	0.86	1.36
Jul-03	31.22	53.92	11.82	2.81	0.23
Aug-03	35.66	49.00	9.67	5.67	0.00
Sep-03	39.21	42.11	11.83	5.86	1.00
Oct-03	18.27	50.97	28.46	0.76	1.53
Nov-03	47.80	43.98	6.67	0.00	1.55
Dec-03	45.44	49.50	1.22	0.00	3.84
Jan-04	28.79	47.38	19.70	0.62	3.51
Feb-04	25.33	42.32	23.86	3.14	5.35
Mar-04	38.22	49.04	5.86	4.15	2.73
Mean	37.10	43.56	15.63	1.99	1.71
StDev	28.31	27.00	21.98	6.25	5.72
Variance	801.60	728.88	483.27	39.02	32.73
Median	35.71	40.00	6.25	0.00	0.00

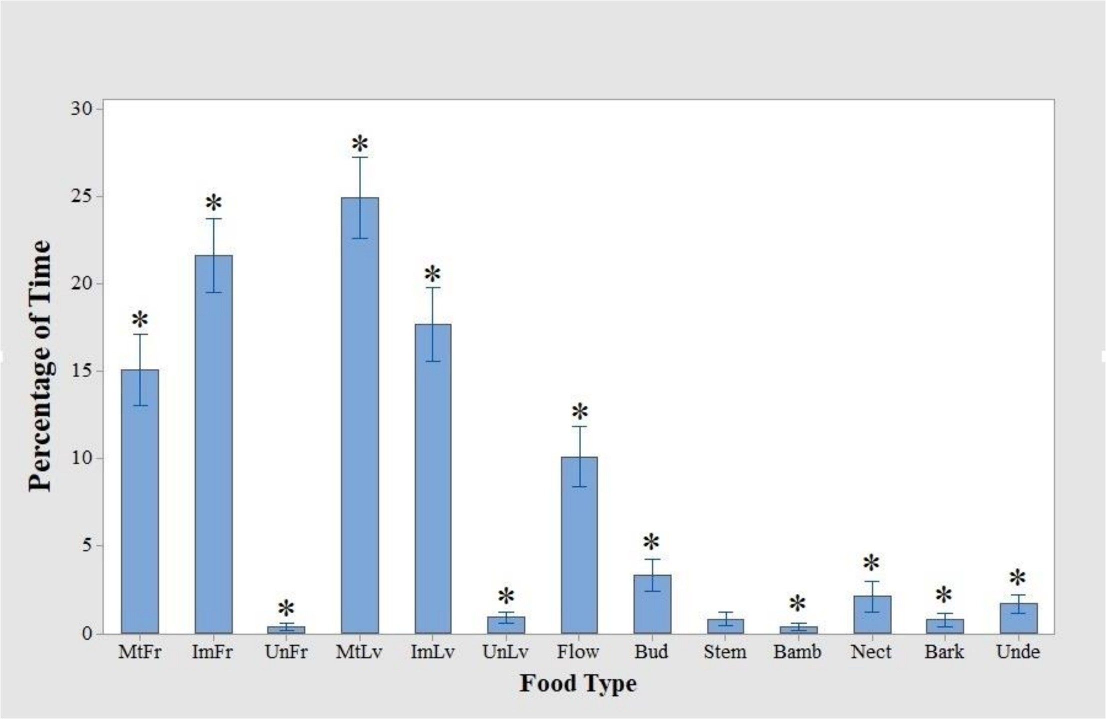

Figure 9*: Diet of the Jaó group in more detail. 95% confidence interval for the mean. MtFr = Mature Fruit, ImFr = Immature Fruit, UnFr = Fruit of Unknown Maturity, MtLv = Mature Leaf, ImLv = Immature Leaf, UnLv = Leaf of Unknown Maturity, Flow = Flower, Bamb = Bamboo, Nect = Nectar, Unde = Undetermined. Asterisks show that the time spent devoted to feeding on a food type varied significantly across sample periods.*

***Table VI**: The overall and intermonthly variation of time devoted to each food type over the entire sample period in percentages. MtFr = Mature Fruit, ImFr = Immature Fruit, UnFr = Fruit of Unknown Maturity, MtLv = Mature Leaf, ImLv = Immature Leaf, UnLv = Leaf of Unknown Maturity, Flow = Flower, Bamb = Bamboo, Nect = Nectar, Unde = Undetermined.*

Sample Period	MtFr	ImFr	UnFr	MtLv	ImLv	UnLv	Flow	Bud	Stem	Bamb	Nect	Bark	Unde
Mar-03	46.65	10.85	2.44	11.79	11.57	2.49	11.30	1.51	0.43	0.36	0.00	0.00	0.63
Apr-03	21.96	7.82	0.28	28.93	9.01	1.29	8.06	4.32	0.00	0.00	18.05	0.00	0.28
May-03	19.50	26.51	0.25	26.85	5.15	0.99	9.48	0.98	0.81	0.00	8.77	0.00	0.70
Jun-03	10.85	38.81	0.00	42.79	1.64	0.22	2.22	1.26	0.00	0.00	0.00	0.86	1.36
Jul-03	8.36	22.67	0.19	51.20	2.71	0.00	10.69	1.13	1.02	0.00	0.00	1.80	0.23
Aug-03	15.58	20.01	0.07	40.88	8.04	0.07	8.27	1.40	0.95	0.00	0.00	4.72	0.00
Sep-03	23.92	15.06	0.22	28.60	13.38	0.13	3.81	8.01	3.09	0.00	0.00	2.77	1.00
Oct-03	9.10	9.18	0.00	17.33	33.52	0.13	17.21	11.25	0.76	0.00	0.00	0.00	1.53
Nov-03	10.58	37.22	0.00	11.84	32.15	0.00	6.30	0.37	0.00	0.00	0.00	0.00	1.55
Dec-03	10.68	34.76	0.00	7.23	39.83	2.45	1.22	0.00	0.00	0.00	0.00	0.00	3.84
Jan-04	5.04	23.75	0.00	11.37	34.48	1.53	15.30	4.40	0.16	0.39	0.00	0.07	3.51
Feb-04	2.97	22.20	0.16	18.68	22.97	0.67	21.40	2.46	1.14	2.00	0.00	0.00	5.35
Mar-04	3.55	34.38	0.29	23.31	23.47	2.25	3.44	2.42	2.10	1.55	0.00	0.50	2.73
Mean	15.08	21.65	0.37	24.95	17.68	0.93	10.13	3.37	0.84	0.37	2.13	0.78	1.71
StDev	22.38	23.19	2.41	25.08	22.88	3.43	18.46	9.91	3.91	2.48	9.70	4.40	5.72
Variance	500.78	537.57	5.80	629.08	523.55	11.75	340.90	98.25	15.26	6.14	94.17	19.35	32.73
Median	0.00	15.00	0.00	18.18	9.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

3.6. Age-Sex Class Variation in Diet

When the Jaó group were analysed as three distinct subsets of groups there was **no** significant difference between the time that they devoted to feeding on any food types (**fruit** *p* value 0.99, **leaf** *p* value 0.99, **flower*** *p* value 0.96, **other** *p* value 0.75, **undetermined** *p* value 0.35) (ANOVA General Linear Model) (**Table VII**; **Fig. 10**; see **Appendix IX**); (**mature fruit** *p* value 0.88, **immature fruit** *p* value 0.91, **fruit of unknown maturity** *p* value 0.38, **mature leaf** *p* value 0.50, **immature leaf** *p* value 0.57, **leaf of unknown maturity** *p* value 0.50, **flower** *p* value 0.82, **bud** *p* value 0.90, **stem** *p* value 0.97, **bamboo** *p* value 0.41, **nectar** *p* value 0.72, **bark** *p* value 0.62, **undetermined** *p* value 0.35 (**Table VIII**; **Fig. 11**; see Appendix **XI**).

Tukey pairwise comparisons of the time each subset spent feeding on different food types can be found in **Appendix X** and **Appendix XII** which shows there were no significant differences were between subsets.

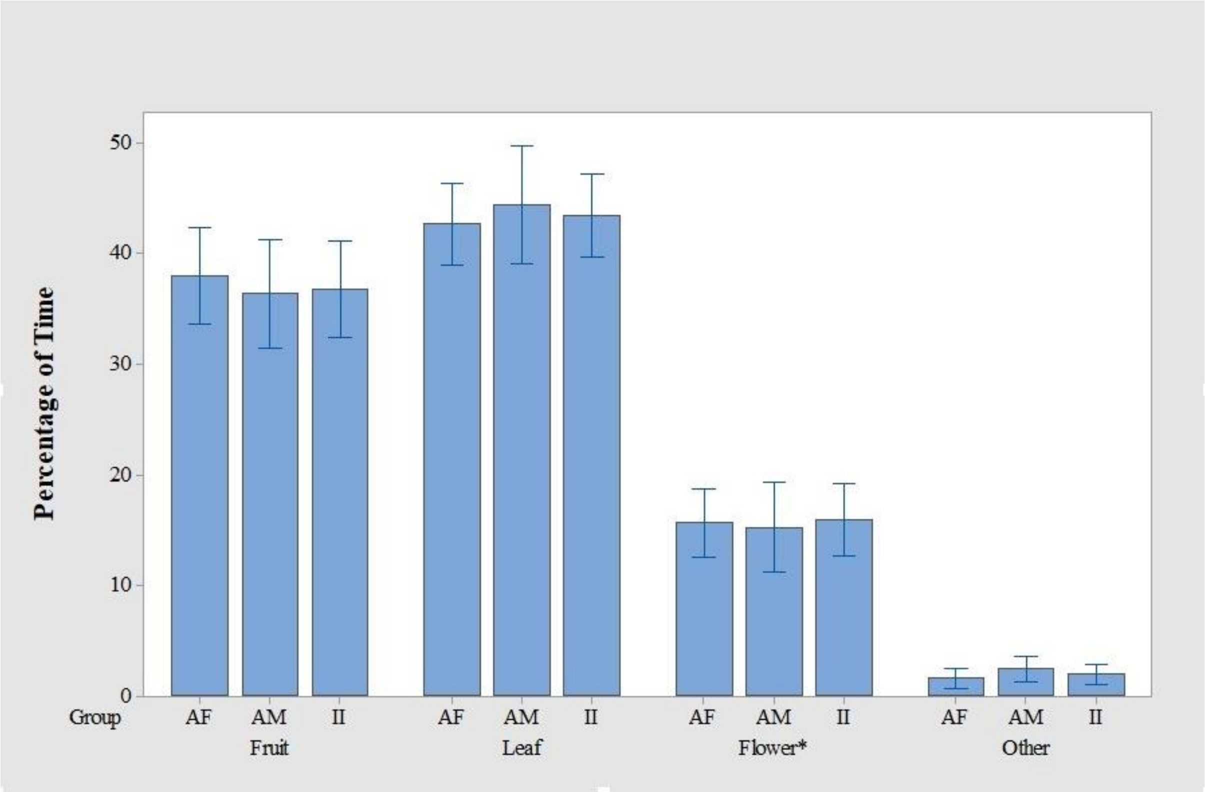

***Figure 10**: Age-sex class variation in diet. 95% confidence interval for the mean. Flower* = flower and flower products. AF = adult females, AM = adult males, II = immature individuals.*

Table VII*: A comparison of the time devoted to feeding on different food types between adult females, adult males, and immature individuals.*

Food Type	Group	Mean	StDev	Variance	Median
Fruit	Adult Female	38.03	27.01	729.39	36.36
	Adult Male	36.44	30.78	947.28	33.34
	Immature Individual	36.83	27.22	740.73	33.34
Leaf	Adult Female	42.73	22.99	528.55	41.20
	Adult Male	44.46	33.49	1121.31	40.00
	Immature Individual	43.48	23.34	544.53	40.83
Flower*	Adult Female	15.66	19.57	382.80	7.69
	Adult Male	15.29	25.70	660.57	0.00
	Immature Individual	15.96	20.33	413.46	9.09
Other	Adult Female	1.61	5.64	31.77	0.00
	Adult Male	2.44	7.51	56.36	0.00
	Immature Individual	1.95	5.40	29.13	0.00
Undetermined	Adult Female	1.98	4.56	20.75	0.00
	Adult Male	1.38	6.38	40.74	0.00
	Immature Individual	1.78	6.09	37.06	0.00

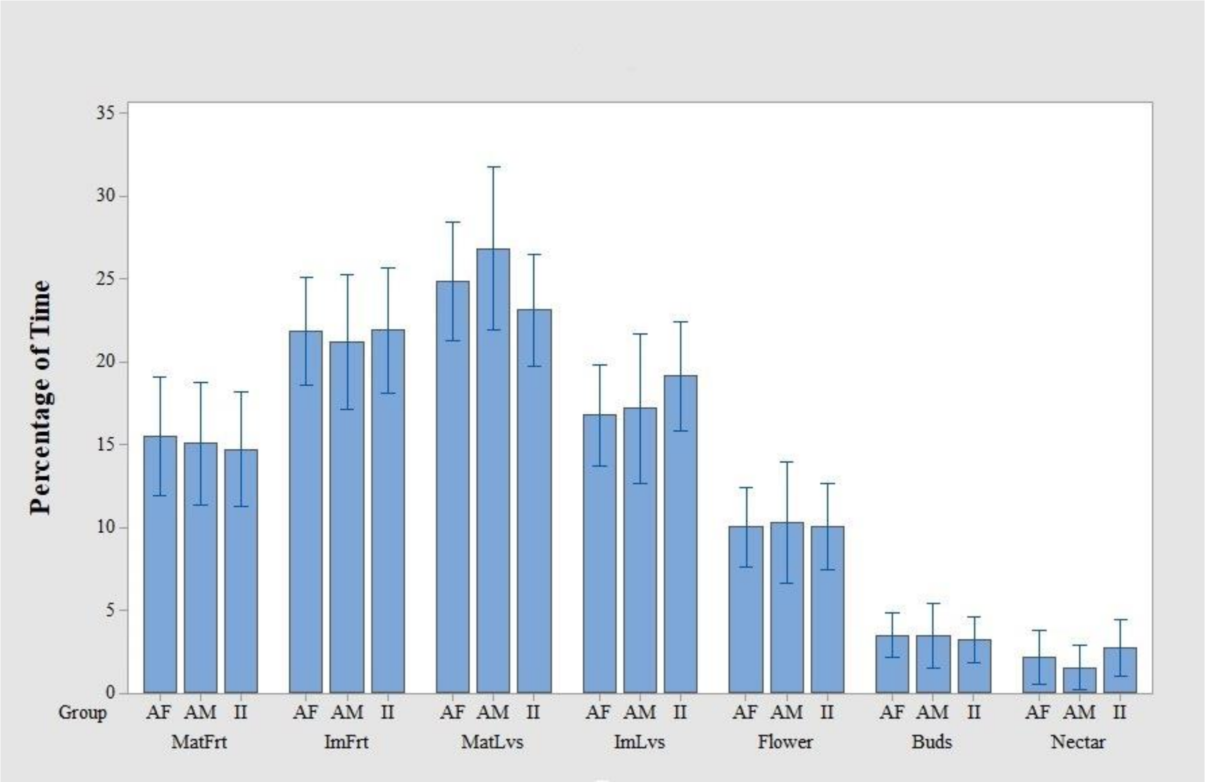

***Figure 11**: Age-sex class variation in diet in more detail. 95% confidence interval for the mean. MatFrt = mature fruit, ImFrt = immature fruit, MatLvs = mature leaf, ImLvs = immature leaf. Does not visualise data from fruit of unknown maturity, leaf of unknown maturity, stem, bamboo, bark, and undetermined. AF = adult females, AM = adult males, II = immature individuals.*

***Table VIII**: A comparison of the time devoted to feeding on different food types between adult females, adult males, and immature individuals.*

Food Type	Group	Mean	StDev	Variance	Median
Mature Fruit	Adult Female	15.48	22.37	500.60	6.90
	Adult Male	15.07	23.39	546.92	0.00
	Immature Individual	14.69	21.54	463.82	4.36
Immature Fruit	Adult Female	21.85	20.43	417.25	18.75
	Adult Male	21.20	25.49	649.88	9.16
	Immature Individual	21.90	23.55	554.45	14.84
Fruit of Unknown Maturity	Adult Female	0.69	3.70	13.65	0.00
	Adult Male	0.17	1.26	1.58	0.00
	Immature Individual	0.24	1.48	2.18	0.00
Mature Leaf	Adult Female	24.88	22.24	494.41	18.18
	Adult Male	26.83	30.85	951.89	20.00
	Immature Individual	23.11	21.03	442.15	16.67
Immature Leaf	Adult Female	16.76	19.03	361.97	11.11
	Adult Male	17.17	28.26	798.71	0.00
	Immature Individual	19.12	20.34	413.53	16.66
Leaf of Unknown Maturity	Adult Female	1.09	3.03	9.20	0.00
	Adult Male	0.46	2.92	8.50	0.00
	Immature Individual	1.25	4.18	17.46	0.00
Flower	Adult Female	10.02	15.08	227.32	0.00
	Adult Male	10.31	23.10	533.62	0.00
	Immature Individual	10.06	16.31	265.92	0.00
Bud	Adult Female	3.50	8.51	72.35	0.00
	Adult Male	3.43	12.22	149.40	0.00
	Immature Individual	3.18	8.62	74.23	0.00
Stem	Adult Female	0.76	4.17	17.42	0.00
	Adult Male	0.95	4.23	17.86	0.00
	Immature Individual	0.80	3.28	10.74	0.00
Bamboo	Adult Female	0.35	1.98	3.93	0.00
	Adult Male	0.60	3.61	13.00	0.00
	Immature Individual	0.17	1.19	1.42	0.00
Nectar	Adult Female	2.14	10.01	100.11	0.00

	Adult Male	1.54	8.33	69.31	0.00
	Immature Individual	2.72	10.71	114.60	0.00
Bark	Adult Female	0.49	3.47	12.06	0.00
	Adult Male	0.88	5.34	28.56	0.00
	Immature Individual	0.97	4.19	17.57	0.00
Undetermined	Adult Female	1.98	4.56	20.75	0.00
	Adult Male	1.38	6.38	40.74	0.00
	Immature Individual	1.78	6.09	37.06	0.00

3.7. Day Range Travel Length

The average day range travel length was calculated for 144 days during the sample period. Estimated distances travelled on the 144 days averaged 1600m ± 942m, with a minimum of 181m and a maximum of 5495m travelled per day (median = 1371m). Day range travel lengths in the rainy season (mean = 1316m ± 585m, median = 1328m, n = 59 days) and the dry season (mean = 1640m ± 908m, median = 1416m, n = 60 days) are significantly different (Two-Sample t-Test: DF = 101, *p* = 0.02) (**Fig. 12**).

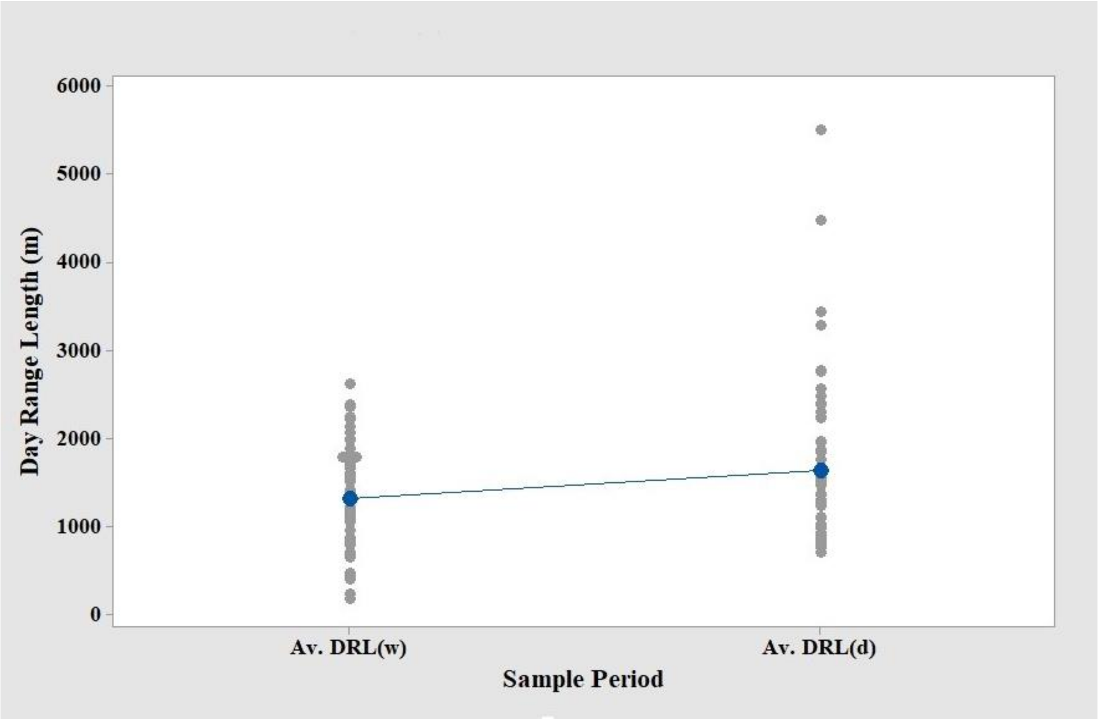

Figure 12*: Individual value pot. Day range travel lengths of the wet (Av. DRL(w)) and dry (Av. DRL(d)) seasons. Av. DRL(w) = Average day range travel length in the wet season. Av. DRL(d) = Average day range travel length in the dry season.*

4. Discussion

4.1. Activity Budget and Feeding Time Comparison

The muriquis of the Jaó group spent most of their time resting, followed by travelling, and then feeding; the same pattern was recorded for the Matão group (**Table IX**; **Fig. 13**). In terms of the percentages, the Matão group devoted more time to resting, travelling, and vocalising than the Jaó group; whereas, the Jaó group devoted more time to feeding, socialising, and engaging in other activities.

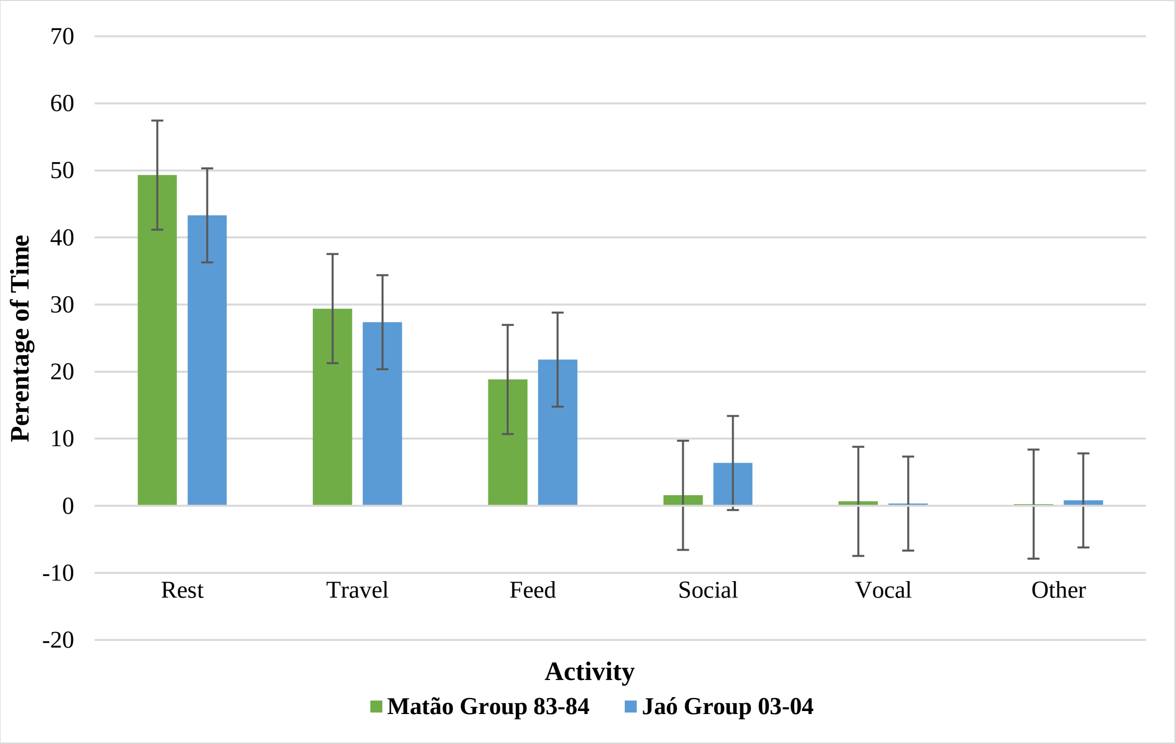

***Figure 13**: The activity budgets of both groups over the respective sample periods. Error bars = standard error.*

***Table IX**: The overall activity budgets of the Matão and Jaó groups over the respective sample periods*

Study	Rest	Travel	Feed	Social	Vocal	Other
Matão Group 1983-84	49.30	29.40	18.83	1.56	0.66	0.25
Jaó Group 2003-04	43.31	27.37	21.79	6.38	0.34	0.81

The activity budget of the Jaó group was similar to time budgets of other muriqui groups, especially when including *B. arachnoides*; resting being the predominant activity, followed by either travelling or feeding (alternating between groups at different sites) (Milton, 1984; Strier, 1987a; de Carvalho *et al.* 2004; Petroni, 2005; Talebi & Soares, 2005; Talebi & Lee, 2010) (**Fig. 14**).

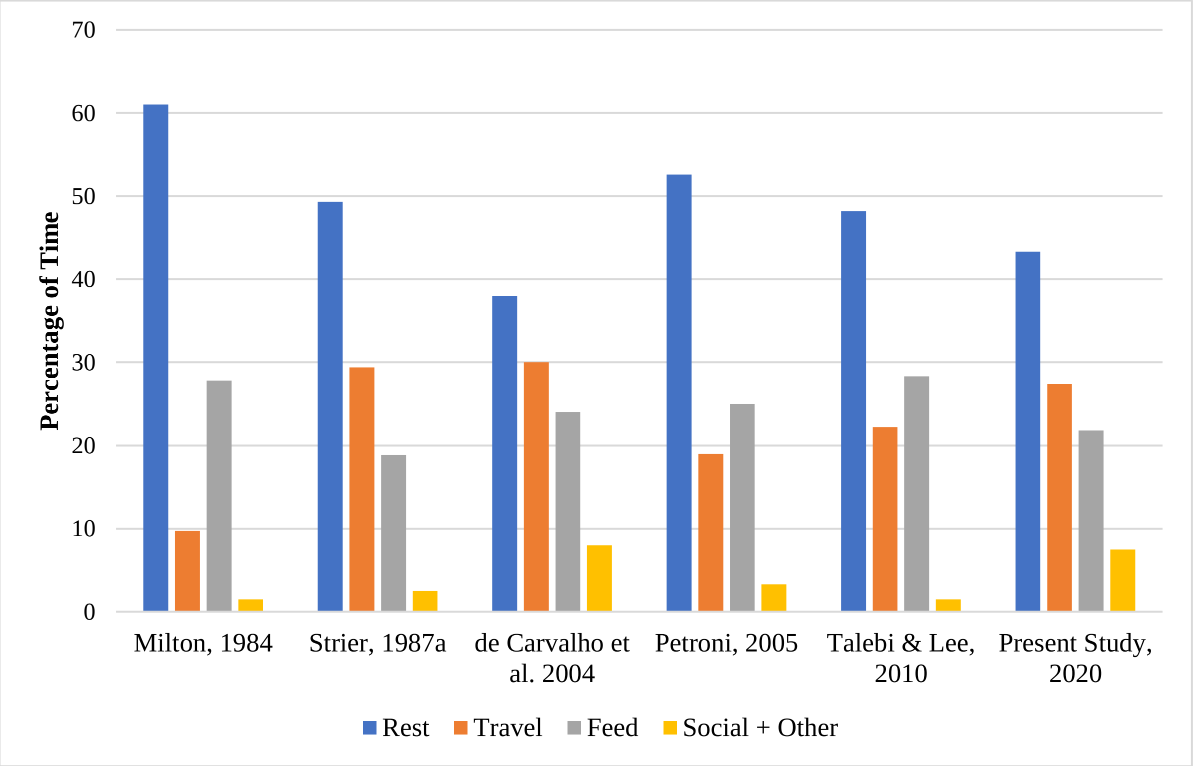

***Figure 14**: The time budgets of muriqui groups including* B. arachnoides, *data from Talebi and Lee, 2010 (**Table III**).*

In terms of feeding time, both groups were similar in the fact that they devoted proportionally the most time to feeding on leaves, followed by fruits, and then flowers and nectar (**Table X**; **Fig. 15)**. Comparatively, the Jaó group devoted more of their time to feeding on fruits than the Matão group (**Table X**; **Fig. 15**). Similar time was devoted to feeding on mature fruits (slightly more for the Jaó group); however, the Jaó group devoted substantially more time to feeding on immature fruits (**Table XI**; **Fig. 16**). A greater percentage of time was recorded for the Matão group feeding on fruits of unknown maturity, which could have impacted the results. If the fruits of unknown maturity are assumed to be mature then the Matão group would have devoted more time than that of the Jaó group (**Fig. 17**). If the fruits of unknown maturity are assumed to be immature fruits then the Matão group would still had devoted less time than the Jaó group to feeding on immature fruits (**Fig. 18**).

The Matão group devoted more time feeding on leaves than the Jaó group overall (**Table X**; **Fig. 15**). Looking at this in more depth, the Matão group devoted more time feeding on immature leaves than the Jaó group, whereas the Jaó group reversely spent more time feeding on mature leaves than the Matão group (**Table XI**; **Fig. 16**). Like with fruits, much more leaves of unknown maturity were recorded for the Matão group. If they were added to the totals of either mature or immature leaves, it would make a noticeable difference. If the leaves of unknown maturity are assumed to be mature then the Jaó group would have still devoted more time to feeding on them than the Matão group, but the difference would not be great (**Fig. 19**). If the leaves of unknown maturity are assumed to be immature leaves then the Matão group would have still devoted more time than the Jaó group to feeding on immature leaves, however, the difference would be a lot more substantial (**Fig. 20**).

The Jaó group devoted more time to feeding on flowers than the Matão group (**Table X**; **Fig. 15**).

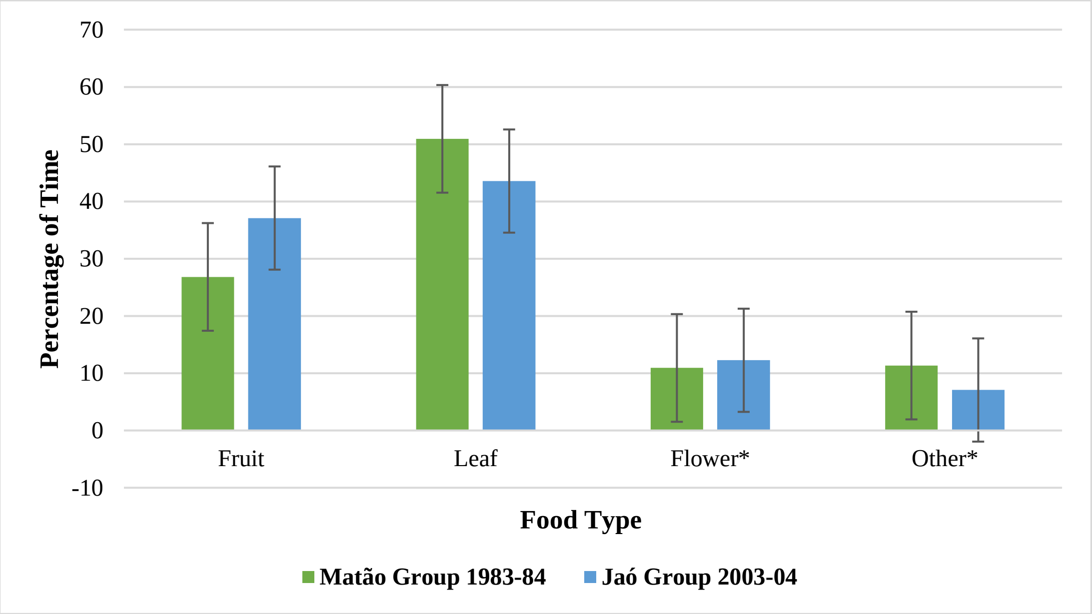

Figure 15*: A comparison of the feeding time of both groups. Flower* = flowers and nectar. Matão group's Other* = bamboo, bark, seeds, buds, and ferns. Jaó group's other = bamboo, bark, buds, stems, and undetermined food items. Error bars = standard error.*

Table X*: The time devoted to each food type by the respective groups. Flower* = flowers and nectar. Matão group's Other* = bamboo, bark, seeds, buds, and ferns. Jaó group's other = bamboo, bark, buds, stems, and undetermined food items.*

Study	**Fruit**	**Leaf**	**Flower***	**Other***
Matão Group 1983-84	26.82	50.93	10.92	11.34
Jaó Group 2003-04	37.10	43.56	12.26	7.07

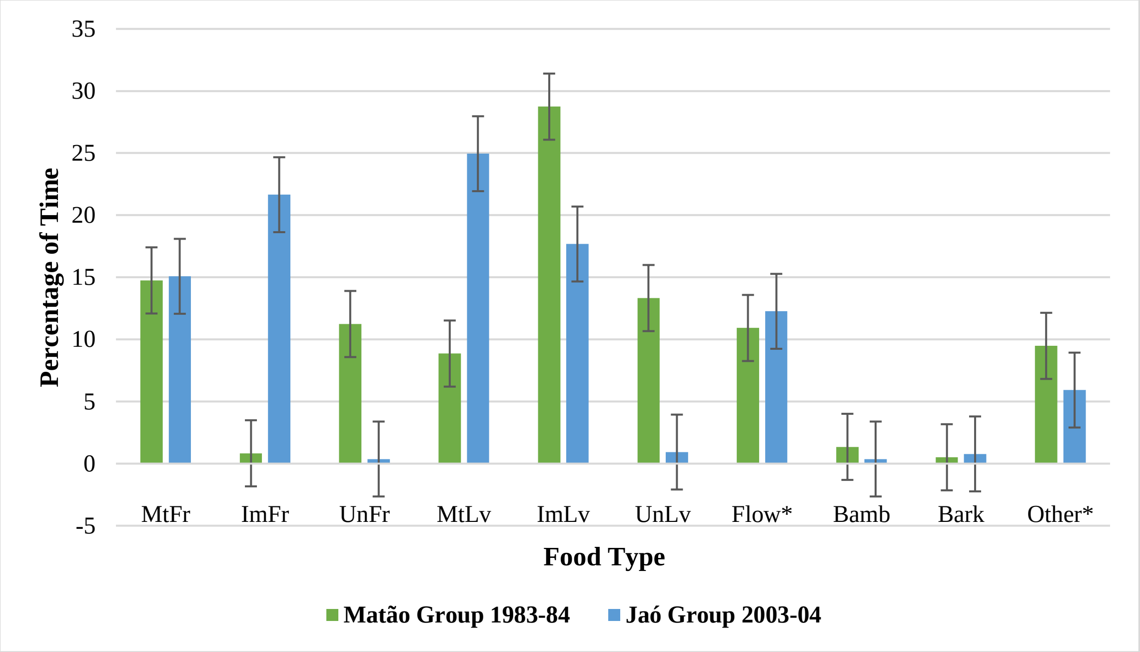

Figure 16: *Feeding time comparison between the Matão and Jaó groups. Flower* = flowers and nectar. Matão group's other = seeds, buds and ferns. Jaó group's other = buds, stems, and undetermined food items. Error bars = standard error.*

Table XI: *Feeding time comparison between both groups. Flower* = flowers and nectar. Matão group's other = seeds, buds and ferns. Jaó group's other = buds, stems, and undetermined food items.*

Food Type	**Matão Group 1983-84**	**Jaó Group 2003-04**
Mature Fruit	14.75	15.08
Immature Fruit	0.83	21.65
Fruit of Unknown Maturity	11.24	0.37
Mature Leaf	8.86	24.95
Immature Leaf	28.74	17.68
Leaf of Unknown Maturity	13.33	0.93
Flower*	10.92	12.26
Bamboo	1.35	0.37
Bark	0.51	0.78
Other*	9.48	5.92

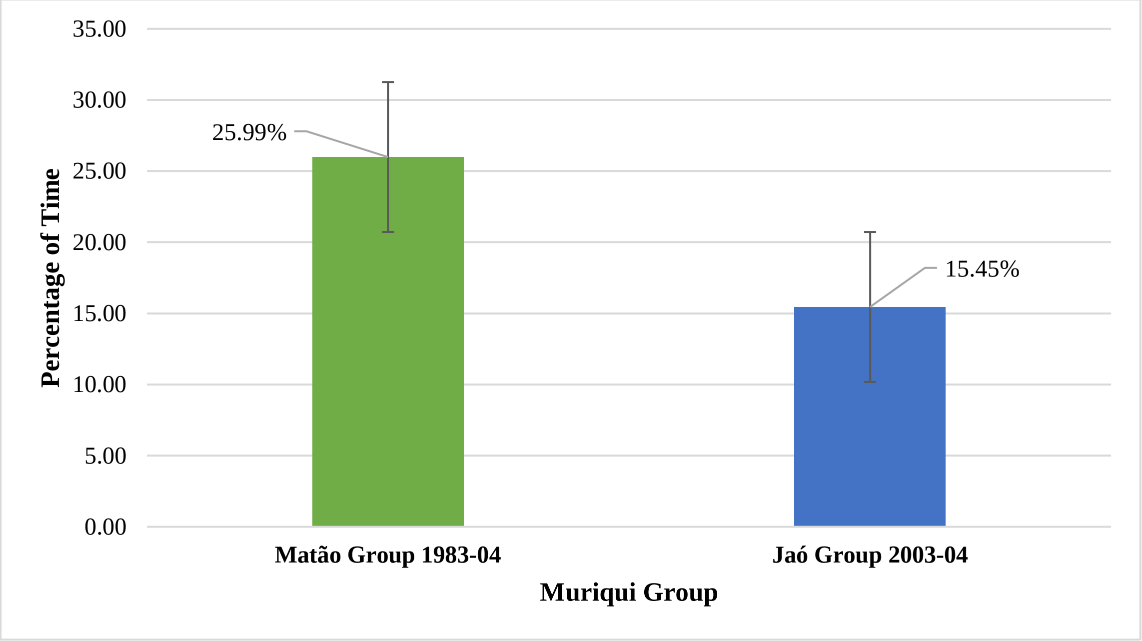

Figure 17*: If fruits of unknown maturity are assumed to have been mature fruits. Matão group:14.75% (mature fruit) + 11.24% (fruit of unknown maturity) = 25.99%. Jaó Group: 15.08% (mature fruit) + 0.37% (fruit of unknown maturity) = 15.45%. Error bars = standard error.*

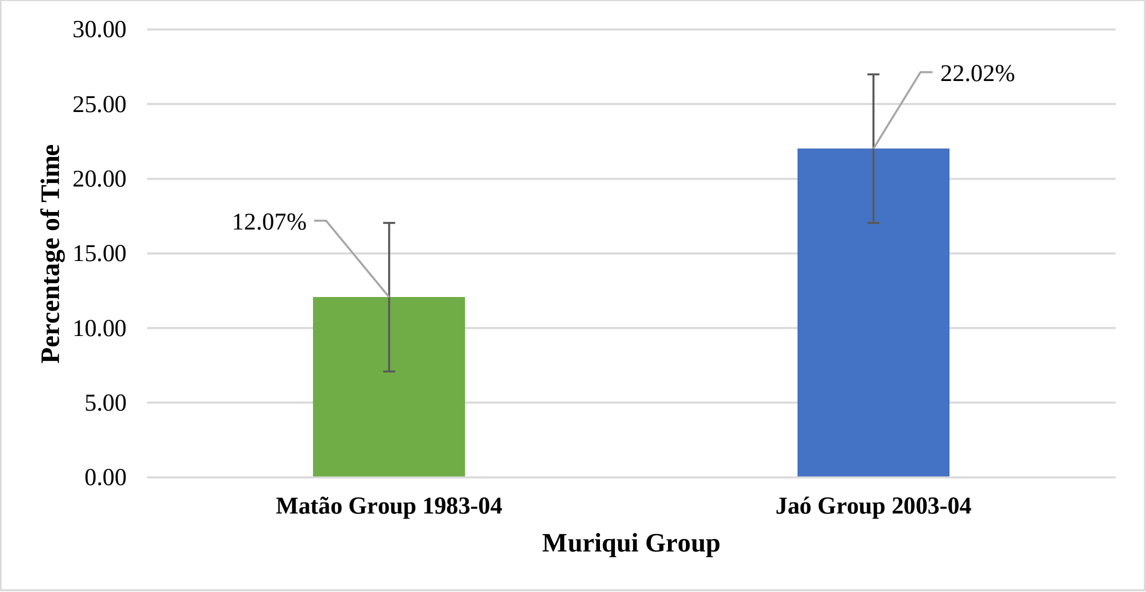

Figure 18*: If fruits of unknown maturity are assumed to have been immature fruits. Matão group:0.83% (immature fruit) + 11.24% (fruit of unknown maturity) = 12.07%. Jaó Group: 21.65% (immature fruit) + 0.37% (fruit of unknown maturity) = 22.02%. Error bars = standard error.*

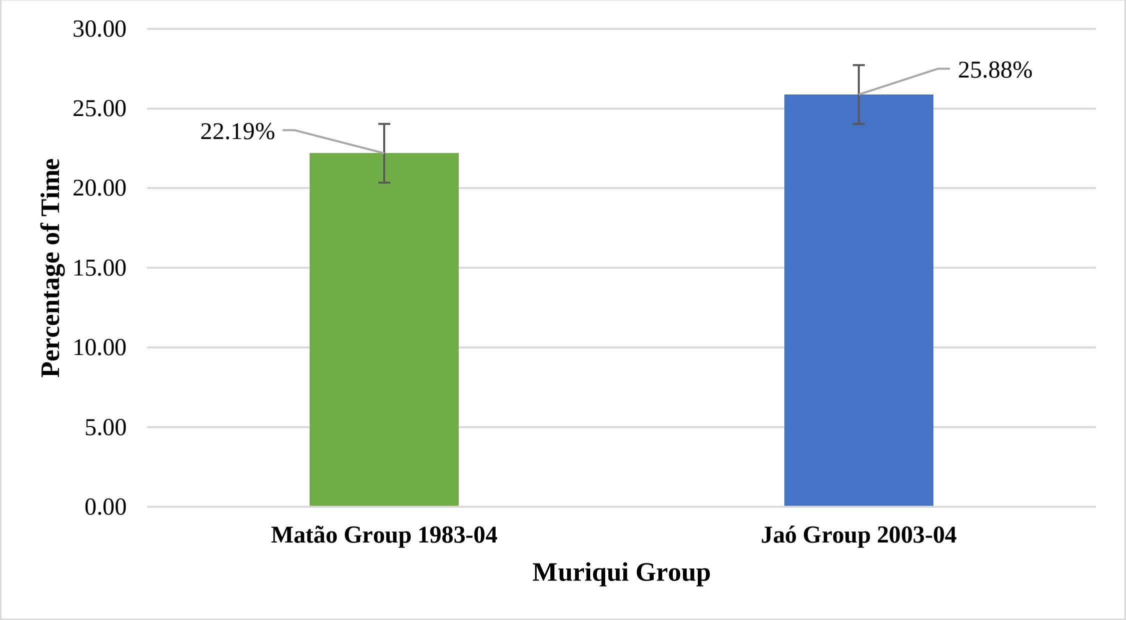

***Figure 19**: If leaves of unknown maturity are assumed to have been mature leaves. Matão group:8.86% (mature leaf) + 13.33% (leaf of unknown maturity) = 22.19%. Jaó Group: 24.95% (mature leaf) + 0.93% (leaf of unknown maturity) = 25.88%. Error bars = standard error.*

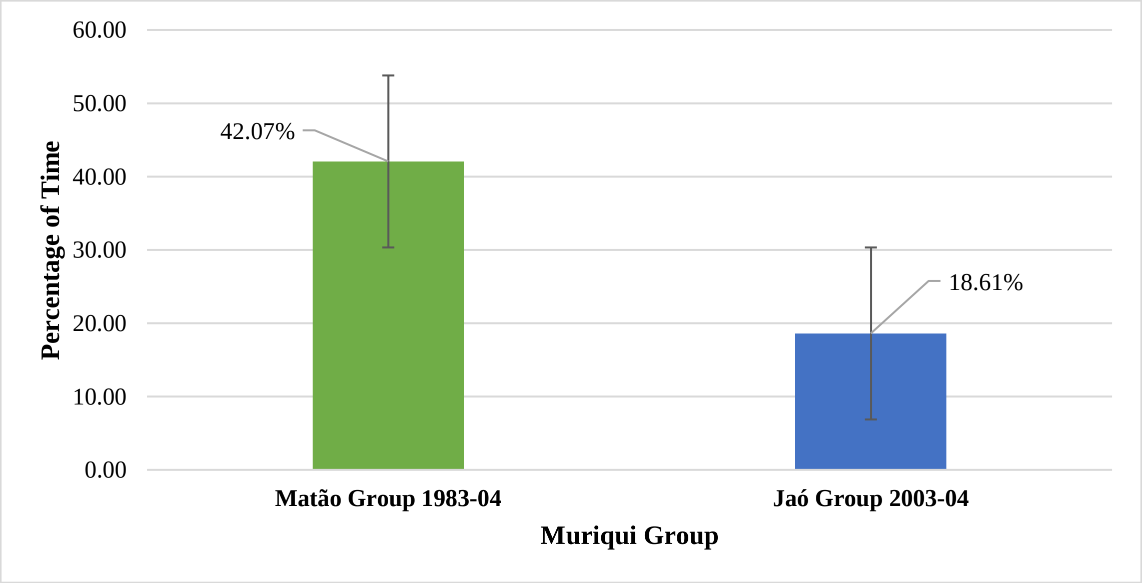

***Figure 20**: If leaves of unknown maturity are assumed to have been immature leaves. Matão group:28.74% (immature leaf) + 13.33% (leaf of unknown maturity) = 42.07%. Jaó Group: 17.68% (immature leaf) + 0.93% (leaf of unknown maturity) = 18.61%. Error bars = standard error.*

It appears that the general activity budget and feeding time analysis patterns were similar for the Matão and Jaó groups regarding the relative proportions of time that they spent on activities and on feeding on different food resources. However, when directly comparing the overall percentages of time each group spent on each activity and on the time each group spent feeding on each food type, differences are apparent.

Greater intragroup feeding competition in the larger Jaó group likely resulted in them having to spend more time feeding and less time resting than the smaller Matão group. The smaller Matão group unexpectedly spent more time travelling than the Jaó group. Perhaps differences in habitat quality of the two group’s respective home ranges influenced the proportion of time the two groups spent travelling. For example, fruits and flower products may have differed in abundance due to forest regeneration and deterioration from edge effects which occurred throughout the years (Strier & Ives, 2012). This could also explain why the Jaó group spent more time feeding on more desirable food resources, comparatively, than the Matão group. The fact that the Jaó group devoted more time to feeding on high energy food resources may have enabled them to travel less as they consumed their daily energy requirements sooner in the day(s). The Matão group’s more folivorous diet possibly contributed to them resting more because leaves lack readily available energy (McNab, 1978). This was the suggestion made by Strier (1987a) used to explain why the larger Matão group rested less when compared to the smaller Fazenda Barreiro Rico group (Milton, 1984).

Even though the Jaó group spent more time feeding on preferred food resources than the Matão group, they also spent more time feeding on leaves (and potentially fruit) of less preferable stages of maturity. Greater intragroup feeding competition may be why the Jaó group spent more time feeding on mature leaves and immature fruits when compared to the

Matão group who spent comparatively more time feeding on immature leaves (and potentially mature fruits). Resources at more preferable stages of maturity would be depleted faster in a larger group, so overall the Jaó group spent more time feeding on preferred food resources but they were of less preferable stages of maturity. Alternatively, differences in group demographics could explain variation in activity budgets and feeding time. One example is that the Jaó group may have spent more time socialising due to greater group size and around three times more immature individuals in the group than what was present in the Matão group (immature individuals spent significantly more time socialising than any other age-sex class within the Jaó group) (**Fig. 7**; **Table II**).

4.1.1. Intermonthly Variation in Activity Budgets and Feeding Time

There were differences in the classification of a sample period between this thesis and Strier's (1987a) study. Strier separated sample periods so that they corresponded with the schedule of phenological sampling from her thesis (Strier, 1986); however, sample periods for this thesis were separated by the months of the year.

The Jaó group's activity budget was highly variable over sample periods, with the exception of time spent vocalising. The Matão group's activity budget **did not** show evidence of intermonthly variation for **any** activity. However, the time devoted to feeding on different food types was highly variable for both the Matão and Jaó groups. The only exception for any group was in the Jaó group, which was the time the group devoted to feeding on stems, which did not vary (overall feeding observations = 0.84%).

The Matão group exploited peaks in flowering during September (*Apuleia praecox*; Leguminosae), February (*Adenocalymna marginatum*; Bignoniaceae), and late April (*Mabea* *fistulifera*; Euphorbiaceae). Mabea was the only flower species in which nectar was eaten exclusively (Strier, 1991). The Jaó group were only recorded feeding on nectar in April and May (greater in April), so they likely exploited the species in a similar manner. The Jaó group also showed peaks in feeding on flower and flower products in October 2003, and January and February 2004; although the species have not been analysed in this thesis.

Both muriqui groups show that the ability to be flexible with their diet (intermonthly variation in feeding time) is essential when living in an environment with seasonal fluctuations in available resources. At least with nectar feeding there is partial evidence that these primates take advantage of high quality foods when they become abundant.

The availability of food resources is regarded as a key stimulus on activity budgets in primate species (Chapman, 1990), and intragroup feeding competition may become incrementally more impactful on activity budgets and feeding time as group size increases; especially during the dry season when preferred food resources become scarcer. Perhaps the larger size of the Jaó group put pressure on the group that the Matão group did not experience during the time that they were being studied. For example, the Matão group’s food resources changed with seasonality availability but they may have been below carrying capacity (Strier, 1991), so the lack of intra-group feeding competition allowed them to maintain a similar activity budget year round. The Jaó group, living closer to carrying capacity, may have had to alter their activity budget as a group in times of fruit and flower scarcity.

Other factors that may have contributed to differences between the two groups include: differences in demographics, rainfall and climatic conditions that may have been different during the two respective time periods, which could have affected fruit and flower availability, and forest composition in terms of tree species might have also changed slightly due to forest generation.

4.1.2. Age-Sex Class Differences in Activity Budgets and Feeding Time

During Strier's study on the diet of the Matão group, the muriqui population at the site appeared to be depressed; resulting in the population potentially being below carrying capacity (Strier, 1991). Strier suggested that during her study period, the diet of the females' may have been "close to optimal" and male diets may have been able to approximate the female diet without any direct competition. Strier suggested that in future observational studies, with population growth, the similarity in the diets between the sexes may show greater variation due to increased feeding competition. This study was consequently carried out 20 years later, in the same forest; albeit, observing a different study group. The Jaó group was more than three times the size of the Matão group during the two respective study periods (**Table XIII**).

It appears that with increased intra-group feeding competition this may not exactly be the case. There was no difference in the time spent feeding on any particular food type between group subsets in the Jaó group. In the smaller Matão group, with less intragroup feeding competition, adult females spent more time feeding on high quality foods than the adult males did (more time devoted to feeding on flowers), whilst they spent the same amount of time as each other feeding overall (activity budget). In the larger Jaó group which faced greater intragroup feeding competition, there was no difference in the time spent feeding on any type of food resource between adult males and adult females. High quality food resources (such as fruits and flowers) would have depleted sooner which likely resulted in the adult females spending more time overall to feeding (activity budget) than the adult males of their group in order to meet the greater metabolic requirements of lactation (Portman, 1970).

There was an almost three-fold size difference in the number of adult females and immature individuals in the Jaó group when compared to the Matão group (**Table XIII**). Strier (1987a) showed that one lactating female devoted more time to feeding than one sexually active but non-pregnant/lactating female; if a larger proportion of the females were lactating in the Jaó group, then this may have been why the Jaó group's females devoted a greater proportion of their time to feeding than the males needed to. Data exists for the reproductive status of the females of the Jaó group during our sample period; it is something to be looked into after the completion of this thesis.

In both groups **no difference** was observed between adult subsets in the time devoted to feeding on fruits or leaves. Strier suggested that the reason for this in the Matão group could have been due to the presence of only one lactating female (more lactating females would perhaps lead to adult females spending more time feeding on fruits and/or leaves). It is likely that there were more lactating females in the Jaó group, but still no difference was observed in the time adult subsets devoted to feeding on fruits or leaves. There was also no difference in the time devoted to feeding on fruits or leaves of varying stages of maturity between adult subsets in the Jaó group; so adult females did not even spend more time feeding on better quality fruits or leaves. Perhaps due to a lack of physical aggression in muriqui society, and the fact that they are sexually monomorphic, no adult subset has an advantage in the acquisition and defending of fruits so feeding times are similar. Feeding competition for leaves, which are a relatively abundant resource, may not even be contested between subsets. Another explanation given by Strier (1991) that could have explained the similarities in feeding time between adult sexes in the Matão group was that preferred fruit resources were not limited during the sample period; which enabled males to devote a similar proportion of their time to fruit without direct competition; which could have been the case for the Jaó group too.

The Jaó group’s adult females travelled less than the adult males; differing from the Matão group in which they travelled the same amount. In both groups the adult females and adult males rested the same amount. Greater intragroup feeding competition in the larger Jaó group which resulted in adult females devoting less time overall to high energy foods but more time to feeding overall, likely also resulted in them travelling less to balance out energy consumption and expenditure. The adult males and females still rested the same amount as each other in the larger Jaó group as the added metabolic cost of lactation that the adult females faced may have had already been accounted for by spending less time travelling.

Immature individuals travelled more and rested less than any adults in both groups. Differences in the energetic demands between adults and immature individuals may account for variances in behaviour when compared to adults (Strier, 1987a); i.e. why they spent more time on energetic activities such as travelling and socialising, and less time resting, in both study groups.

The majority of the immature individuals’ social behaviour in the Jaó group can be accredited to play behaviour; it looks as if it may have been the same case in the Matão group also, however, this is not specified (in Strier, 1987a). Adult males spent more time socialising than adult females in the Jaó group. It does not specify whether this was the same for adults in the Matão group (Strier, 1987a); however, Strier (1999) stated that most embraces are between adult females, followed by adult female-adult male. The direction of social behaviour has not been analysed for the Jaó group, so it cannot be confirmed whether adult male social interactions were male-male, male-female, or male-immature.

In the Jaó group, immature individuals devoted a similar proportion of time to feeding on each food type as the adults and also spent a similar amount of time feeding overall to the adult males. The fact that immature individuals spent a similar amount of time feeding on high energy foods when compared to the adults in the Jaó group, in conjunction with a similar amount of time feeding overall to the adult males, points towards the possibility that the metabolic stress of growing for immature individuals is similar to that of larger individuals who do not have the added metabolic stress of lactation (males and non-reproductive females).

In the Jaó group, immature individuals and adult females vocalised more than adult males; perhaps immature individuals and adult females vocalised more than adult males due to their maternal-infant relationships; although the direction of vocalisations have not been analysed in this thesis. Strier (1987a) does not state whether there was an age-sex class difference in time devoted to vocalising in the Matão group. According to Strier (1987a) observational biases (due to smaller individuals being more conspicuous and adults being easier to see) may have resulted in some of the differences in the activity budgets of adults and immatures; this could have been the case with the Jaó group's observations too.

Adult females of the Jaó group were engaged in "other" activities more than adult males and immature individuals. Although not specifically stated, it appears (**Fig. 3** in Strier, 1987a) that immature individuals were engaged in other activities more than both adult sexes in the

Matão group. The Matão group's adult males and adult females may have devoted a similar proportion of their time to "other" activities when compared. It is difficult to theorise why the Jaó group's adult females spent more time on "other" activities than the other subsets. Perhaps if there was more lactating adult females in the Jaó group then they had to spend more time drinking water, however my suggestion is only tentative. Rainfall and climatic conditions for our study period could provide added insights into this result as it would have impacted the behaviours of the monkeys.

The activity budget and feeding time analysis of the Jaó group's females (using their reproductive statuses during the study period) can be explored after the completion of this thesis to provide a better insight into the effects of lactation on the behavioural ecology of adult female northern muriquis.

4.2. Diurnal Activity Cycles Comparison

The overall average diurnal activity cycles of the Matão and Jaó groups are very similar; with both groups resting during the late morning to mid-afternoon, then later a distinct decline in rest and an increase in feeding late in the afternoon. Both groups showed peaks in feeding in the early morning and late afternoon; a pattern also observed in southern muriquis (Talebi & Lee, 2010) which is possibly a strategy used to maximise energy intake in relation to the energetic requirements required for overnight fasting (Talebi & Lee, 2008). Talebi and Lee (2010) suggest this pattern is common as an adaptation to high temperature variation. Resting and feeding were inversely related throughout a typical day for the Matão group, this appears to be the case also for the Jaó group. Social activity seemed to increase as resting increased for the Jaó group, apart from the first hour of observations. Perhaps the monkeys, whilst resting in closer proximity to other group members, used the opportunity to strengthen social bonds by way of embracing and other close contact behaviours.

4.2.1. Seasonal Variation in Diurnal Activity Cycles

The number of months used as the sample for each group varied (**Matão** group: wet and warm months = **December, January, February**; dry and cold months = **May, June, July**. **Jaó** group: wet and warm months = **November, December, January, February, March**; dry and cold months = **May, June, July, August, September**).

It is apparent that both groups shifted the timing of their behaviours between seasons. The wet season diurnal activity cycle of both groups looked similar when compared. The main difference was seen when comparing the dry season diurnal activity cycle of each group; in which the Jaó group's larger size may have influenced their behaviour.

During the warm wet season, the Matão group rested during the mid-afternoon hours during the hottest part of the day. This pattern differed in the cold dry season; when they remained inactive until the midday hours. Greater energetic demands are placed on homeothermic species in colder conditions in order to maintain a stable body temperature and so the Matão muriquis seemed to remain inactive throughout the mornings in the dry season to conserve warmth acquired throughout the night (Strier, 1986). Heat stress may have a similar impact on their energetic demands in order to regulate cooling of the body (Strier, 1986); the Matão muriquis rested during the hottest part of the day in the wet season to adapt to this pressure.

The Jaó group also rested during the mid-afternoon hours during the hottest part of the day in the wet season. Similarly, the Jaó group remained inactive during the mornings of the dry season, but they typically became active earlier in the day than the Matão group did. A spike in travel and feeding, accompanied by a decline in rest, would occur from 09:00-10:59. Perhaps due to greater intra-group competition for resources, the larger Jaó group would deplete the local food resources sooner and would be required to travel earlier in the day to feed. Both groups showed an increase in rest during the midday to mid-afternoon hours in the dry season; perhaps once again to conserve energy after feeding.

As stated in **4.1.1.** the Jaó group, in contrast to the Matão group, did show high intermonthly variation in their activity budget over sample periods. So, unlike the Matão group who appeared to shift **only** the timing of their activities between seasons, the Jaó group shifted both the proportion of time they devoted to activities **and** the timing of their activities between seasons. Strier (1987a) suggested that seasonal variation in food availability did not appear to alter the Matão group's activity budget over sample periods, however, she said it could have caused them to shift the timing of their activities between sample periods. Greater intra-group competition for seasonally reduced resources may have contributed to the Jaó group having to alter **both** their activity budgets and diurnal activity cycles between seasons.

The population density was much greater at the RPPN-FMA during 2003-04, as opposed to in 1983-84, so the Jaó group may have had to fluctuate their diurnal activity cycle to a greater extent between seasons in order to fulfil the needs of the individuals within their larger group (within a larger population) and in a more saturated habitat.

Alternatively, the fact that I included five months instead of three months for each season may have impacted the data of the diurnal activity cycles due to a broader range of climatic conditions throughout a five month period as opposed to a three month period.

Climate, rainfall, and phenology data for this time period could also provide further insights into why there are differences in the diurnal activity cycles between seasons and between the groups; especially when it pertains to the dry season differences.

4.3. Day Range Travel Length Comparison

Day range travel lengths are thought to increase as group weight/size increases in order for individuals to fulfil their daily energy consumption requirements (Clutton-Brock & Harvey, 1977b). However, the Matão group of muriquis actually travelled less daily (median) (**Table XII**) as their group size increased from 23 to 67 (Strier, 1987b; Dias & Strier, 2003) (**Table XIII).** The Jaó group of this study was the largest in size comparatively and had the largest median day range travel length. The fact that the intermediately sized Matão group from Dias and Strier's (2003) study had the shortest day range travel length could be due to them being closer to optimal size. The smaller Matão group from Strier (1987b) may have had a larger day range travel length than the larger Matão group from Dias and Strier (2003) due to differences in home range habitat quality (resource abundance) or the threat posed by predators (Markham *et al.* 2015). The Jaó group may have had a larger day range travel length due to greater intra-group feeding competition within the group or also as a result of relatively poorer habitat quality than the Matão group from either study period.

The Matão group almost tripled in size and doubled in the median number of individuals within subgroups between Strier (1987b) and Dias and Strier (2003), in doing so shifted from a very cohesive group to a one that tended to utilise fission-fusion. Dias and Strier suggest this may be a reflection on the limit of individuals a single group can maintain whilst foraging before having to split up. Data on group cohesion during the present study would provide further insights into how larger groups adapt to the challenges of increasing intra-group feeding competition.

***Table XII**: The day range travel lengths of the Matão and Jaó groups in different study periods. Matão 1983-84 are the study group in Strier, 1987b; Matão 1998-99 are the study group in Dias & Strier, 2003; Jaó 2003-04 are the study group in the present study. DRL = Day Range Travel Length. SD = Standard Deviation. N = Number of Days.*

Values	Matão 1983-84	Matão 1998-99	Jaó 2003-04
Average DRL	1283m	1313m	1600m
DRL Min and Max	141m and 3403m	200m and 2835m	181m and 5495m
SD	642m	573m	942m
Median	1248m	1206m	1371m
N	84	144	144
Wet DRL	1427m	1358m	1316m
SD	597m	532m	585m
Median	1407m	1318m	1328m
N	58	72	59
Dry DRL	960m	1269m	1640m
SD	631m	613m	908m
Median	862m	1132m	1416m
N	26	72	60

***Table XIII**: The demographics of the respective groups during different study periods. Matão 1983-84 are the study group in Strier, 1987b; Matão 1998-99 are the study group in Dias & Strier, 2003; Jaó 2003-04 are the study group in the present study. Data from Dias & Strier, 2003 **Table I**. *The Matão group's size dropped to 57 during some months.*

Study Group	Adult Males	Adult Females	Immatures	Total
Matão 1983-84	6-8	8-9	9-10	23-27
Matão 1998-99	13-14	19	30	57*-63
Jaó 2003-04	25	31	32	88

No seasonal variation in day range travel length was observed for the Matão group during either study period (Dias & Strier, 2003), whereas there was seasonal variation in the Jaó group's day range travel lengths. Dias and Strier revealed no evidence of a relationship between group size and day range travel length between seasons; however, the larger Jaó group did show seasonal variation in day range travel length.

Dias and Strier suggested the Matão group's lack of interseasonal differences in day range travel length may be due to higher per capita travel costs in the dry season. Perhaps the degree of difference in group size influenced the two group's strategies in the dry season differently. The smaller Matão group(s) may have been able to persist for longer on smaller patches of fruits, which enabled them to conserve energy and travel no more in the dry season than in the wet season. Whilst the Jaó group had to travel more because they depleted food resources sooner and had more individuals to feed (as suggested for them becoming active earlier in the day in the dry season (dry season diurnal activity cycle)).

One alternative is that the Jaó group's home range may have had wider dispersed fruit and flower sources, which may result in differences in day range travel lengths. Home range size was not explored for the current study due to time constraints, but this could be very informative in the description of the Jaó group's day range travel length and important in analysing the differences seen when comparing it with the Matão group's day range travel lengths during both of the other studies (Strier, 1987b; Dias & Strier, 2003; and in Lima *et al.* 2019).

Another alternative is that the difference in group demographics contributed to the differences in ranging patterns. Muriquis at RPPN-FMA have been shown to adapt to increases in population density and habitat saturation by becoming more terrestrial (Tabacow *et al.* 2009; Strier & Ives, 2012), however, increasing day range travel lengths could be another alternative to enable the consumption of sufficient resources. The Jaó group in 2003-04 would have been functioning within a more saturated habitat than what the Matão group in 1983-84 was, so they may have had to travel farther as a group, comparatively, in order to fulfil their daily energetic requirements.

4.4. Conclusion

The difference in group size appears to have contributed to differences in the behavioural ecology between the Matão and Jaó groups. The reason for this is that as group size increases it creates more pressure by way of intragroup competition for food resources which forces the group of individuals to adapt their behaviours in ways a smaller group would not have to.

The Jaó group spent more time feeding and less time resting than the Matão group as predicted. The larger Jaó group likely faced greater intragroup competition for resources which resulted in them having to spend more time feeding and less time resting than the smaller Matão group. My prediction that the Jaó group would travel more was, however, not supported. The Matão group may have spent more time travelling/moving around due to a lesser abundance of high energy fruit and flower resources. The Jaó group in turn could have spent less time travelling if fruits and/or flowers were more abundant, as they fulfilled their daily energy requirements sooner by spending more time feeding on fruits and flower products.

My prediction that the Jaó group would spend more time feeding on less desirable foods than the Matão group was also not supported. I believed that increased feeding competition for preferred food resources would result in the group spending relatively more time feeding on leaves and “other” food types. Differences in the abundance of fruit and flower (and flower products) within each group’s home range may have influenced the feeding time of each group; perhaps the Jaó group had greater fruit and flower resource availability. This may have also contributed to the Jaó group travelling less as they consumed their daily energy requirements sooner in comparison to the Matão group due to the higher energy content of fruits. Greater folivory in the Matão group may have also contributed to the smaller group spending more time resting.

Although the Jaó group spent more time feeding on fruits and flowers (and flower products) overall, when looking at the time devoted to feeding on these resources and their stage of maturity there is an interesting observation. Greater intragroup feeding competition might explain why the Jaó group spent more time feeding on **mature** leaves than the Matão group did; less preferable over **immature** leaves. The Jaó group spent more time feeding on both **mature** fruits and **immature** fruits than the Matão group (however, if the fruits of unknown maturity are **assumed to be mature** then the Matão group would have devoted more time to them than the Jaó group). Food resources of preferential maturity would deplete faster in a larger group, so this may explain these results.

Intragroup feeding competition may become incrementally more impactful on activity budgets and feeding time as group size increases; especially during the dry season. Both groups showed high intermonthly variation in feeding time due to seasonal fluctuations in food resources. The Matão group was potentially below carrying capacity during Strier’s study period and thus was able to keep their activity budget stable between seasons due to a lack of intragroup feeding competition. The activity budget of the Jaó group, however, varied intermonthly; which could have been the result of greater intragroup feeding competition for seasonally reduced fruits and flowers.

The Matão group were able to keep their activity budget stable between seasons, however, they did have to shift the timings on their activities between seasons (diurnal activity cycles). The Jaó group showed intermonthly variation in **both** their activity budget and diurnal activity cycles between seasons. The general pattern of each group's diurnal activity cycle looked similar when comparing the averages of a 12+ month period, however, the differences became more pronounced when comparing the respective dry seasons. The behavioural strategy of remaining inactive in the cold dry season mornings appeared to have occurred in both groups, but the Jaó group had to become active sooner to feed. This may have been due to the increased intra-group competition for resources in the larger Jaó group whom depleted the local food resources sooner which resulted in them having to become active earlier in the day.

My prediction that the Jaó group would have a larger day range travel length was supported. A larger group has to exploit a larger area for food resources in order to fulfil the needs of more individuals. A small group like the Matão from Strier's (1987b) study may travel more than an intermediate group due to greater predation pressures. Alternatively, the quality of habitat that each group experienced, and/or differences in demographics, may have influenced the results. Optimal group size may be around 57-63 individuals like in Dias and Strier's study (2003).

My prediction about the Jaó group having to travel more in the dry season than in the wet season was also supported. Greater intragroup feeding competition for local resources in the dry season likely resulted in the Jaó group having to travel greater distances in the dry season than they had to in the wet season. The smaller Matão group, whom may have been living below carrying capacity and experiencing a lack of intragroup competition, was able to persist for longer on smaller patches of fruits which enabled them to conserve energy and travel no more in the dry season than they had to in the wet season.

In terms of my predictions based on specific differences between male and female metabolic needs due to lactation, some but not all of my predictions were supported. My prediction that adult females of the larger Jaó group would spend more time feeding than the adult males of the group was supported, but my prediction that they would also spend more time feeding on preferred foods was unsupported. It appears that greater intragroup feeding competition for preferred food resources in larger groups is an influence of these differences in behavioural ecology. In smaller groups where there is less intragroup feeding competition, adult females and adult males can spend the same amount of time feeding overall because adult females are able to devote more of their time to feeding on higher energy food types (flowers in the Matão group). As group size increases and intragroup feeding competition for preferred food resources also increases, adult females instead have to devote more time feeding overall (as seen in the Jaó group).

My prediction that the Jaó group's adult females would travel less than the adult males was also supported. Greater intragroup feeding competition in larger groups seems to result in adult females, who are unable to spend enough time feeding on high energy foods, feeding more and travelling less overall to balance out energy consumption and expenditure to meet the needs created by the added metabolic stress of lactation. My prediction that the Jaó group's adult females would rest more than the adult males was not supported; like in the

Matão group they rested for a similar amount of time. Perhaps because adult females travelled less and spent more time feeding than the adult males, they did not also require more rest; the added metabolic cost of lactation had already been accounted for.

I believe all of these results show that my hypothesis on the importance of group size was overall supported. Group size was larger for the Jaó group so they faced greater intragroup feeding competition, and due to this difference, the behavioural ecology of the Matão and Jaó groups differed.

This type of study is important because it enables insights into how different sized groups adapt their behavioural patterns in order to fulfil their daily energetic needs. Seasonal shifts in resource availability appears to place a greater stress on groups of a larger size. Smaller groups may be able to maintain their activity budget year round, something larger groups may be unable to do. Implications for conservation include providing more evidence that even by 2003-04 the population was closer to carrying capacity than it was in 1983-84. The population size had increased, and within group competition for the Jaó group appeared greater than what the Matão group faced in 1983-84 (highlighted by the greater time that the Jaó group spent feeding on immature fruits and mature leaves, their longer day range travel length, and having to vary their activity budgets, day range travel length, and their diurnal activity cycle across sample periods (more than the Matão group had to) in response to seasonally reduced resources). Habitat expansion, if and where possible, would be highly beneficial to the long-term health of the population.

As mentioned in the introduction, the demographics were very different between groups and between study periods; with around 50 individuals split into two groups between 1983-84, and over 200 individuals split into four groups between 2003-04. Fluctuations in population demographics can affect the composition of groups, as well as the number of groups and their sizes (Strier *et al.* 2006). Due to the isolated nature of the RPPN-FMA, the population growth that occurred between study periods may have created demographic stresses (Strier & Ives, 2012) that the Jaó group experienced more so than did the Matão group. These stresses may have also contributed to the variations observed in the behavioural ecology of the two groups. Increases in both fertility and in the mortality of prime-aged individuals since 1983-84 have likely influenced the behaviour of muriquis in this population also (Strier & Ives, 2012). Behavioural changes exemplified later by the Matão group expanding their vertical niche, especially feeding and travelling more terrestrially, are likely an adaptation to demographic and ecological stresses (Tabacow *et al.* 2009). Immature individual sex ratios were different during the study periods, with it being female biased during 1983-84 and male biased during 2003-04 (Strier *et al.* 2006); which alters the dynamics of the population and groups over time. Infant mortality rates for both sexes from 0-1 and 1-2 years of age were greater between 2003-04; which is a sign that carrying capacity at the RPPN-FMA was actually even lower than previously estimated (Strier *et al.* 2006). Again, another possible factor that could have influenced the behavioural ecology of the two groups was the variances in the home ranges habitat quality during the respective study periods. This could have impacted day range travel lengths if food resources differed in abundance, diversity, and distribution; which could in turn impact activity budgets, feeding time, etc. Increasing the available habitat for the population at the RPPN-FMA could help to alleviate some of the ecological pressures that the groups there are facing from overcrowding (Strier & Ives, 2012). Group size was focused on as the main comparative variable for the purposes of this thesis but the influence of demographic and habitat differences undoubtedly also contributed to the behavioural differences that were presented here. Rainfall and climatic conditions may have also influenced these data.

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Appendices

Appendix I.

The output of the general linear model (activity budget); specifically, the analysis of variance. Displayed here are the degrees of freedom (DF), F-Value, and P-Value.

Activity	Source	DF	F-Value	P-Value
Rest	Sample Period	12	2.84	0.00
Travel	Sample Period	12	5.89	0.00
Feed	Sample Period	12	4.76	0.00
Social	Sample Period	12	11.06	0.00
Vocal	Sample Period	12	1.64	0.07
Other	Sample Period	12	1.86	0.03

Appendix II.

Tukey Pairwise Comparisons of the sample periods (activity budget) (grouping information using the Tukey Method and 95% confidence) are listed below to show where the significant differences were over the sample periods (sorted by the highest mean in descending order). Means that do not share a letter are significantly different.

Activity	Sample Period	N	Mean	Grouping			
Rest	Dec-03	15	49.38	A	B		
	Sep-03	38	48.94	A			
	Oct-03	42	47.21	A	B		
	Jun-03	31	46.57	A	B		
	Feb-04	42	46.54	A	B		
	Jan-04	45	46.14	A	B		
	Mar-04	36	44.57	A	B		
	Nov-03	27	43.05	A	B		
	May-03	33	42.82	A	B		
	Aug-03	34	39.62	A	B		
	Apr-03	42	39.23	A	B		
	Mar-03	51	37.83	A	B		
	Jul-03	48	36.84		B		
Travel	Aug-03	34	37.66	A			
	Mar-03	51	34.40	A	B		
	Jul-03	48	32.39	A	B	C	
	Apr-03	42	31.43	A	B	C	D
	May-03	33	28.93	A	B	C	D
	Nov-03	27	25.58		B	C	D
	Dec-03	15	25.49	A	B	C	D
	Jun-03	31	24.77		B	C	D
	Jan-04	45	23.37			C	D
	Feb-04	42	22.59				D
	Sep-03	38	21.90				D
	Oct-03	42	21.86				D
	Mar-04	36	21.77				D
Feed	Mar-04	36	27.06	A			
	Jul-03	48	26.38	A			
	Sep-03	38	24.99	A	B		
	Feb-04	42	24.85	A	B		

	Jun-03	31	24.58	A	B			
	Jan-04	45	22.53	A	B	C		
	Oct-03	42	22.33	A	B	C		
	Nov-03	27	22.26	A	B	C		
	Aug-03	34	20.95	A	B	C		
	Dec-03	15	20.92	A	B	C		
	Apr-03	42	16.51		B	C		
	May-03	33	16.25		B	C		
	Mar-03	51	14.87			C		
Social	Apr-03	42	12.09	A				
	Mar-03	51	11.28	A	B			
	May-03	33	10.88	A	B	C		
	Oct-03	42	7.72	A	B	C	D	
	Nov-03	27	6.39		B	C	D	E
	Jan-04	45	6.08			C	D	
	Mar-04	36	5.70			C	D	E
	Feb-04	42	4.61				D	E
	Sep-03	38	3.64				D	E
	Jul-03	48	3.51				D	E
	Dec-03	15	3.38				D	E
	Jun-03	31	3.23				D	E
	Aug-03	34	0.99					E
Vocal	Nov-03	27	1.00	A				
	May-03	33	0.58	A	B			
	Feb-04	42	0.53	A	B			
	Jun-03	31	0.47	A	B			
	Apr-03	42	0.38	A	B			
	Dec-03	15	0.37	A	B			
	Jan-04	45	0.35	A	B			
	Mar-04	36	0.32	A	B			
	Oct-03	42	0.28	A	B			
	Mar-03	51	0.24	A	B			
	Jul-03	48	0.21	A	B			
	Aug-03	34	0.01		B			
	Sep-03	38	0.00		B			
Other	Nov-03	27	1.72	A				
	Jan-04	45	1.52	A				
	Mar-03	51	1.37	A				
	Feb-04	42	0.89	A				
	Aug-03	34	0.77	A				
	Jul-03	48	0.66	A				
	Oct-03	42	0.61	A				

	Mar-04	36	0.58	A
	May-03	33	0.54	A
	Sep-03	38	0.53	A
	Dec-03	15	0.47	A
	Jun-03	31	0.38	A
	Apr-03	42	0.34	A

Appendix III.

The output of the general linear model (activity budget; age-sex class differences); specifically, the analysis of variance. Displayed here are the degrees of freedom (DF), F-Value, and P-Value.

Activity	Source	DF	F-Value	P-Value
Rest	Group	2	54.69	0.00
Travel	Group	2	29.84	0.00
Feed	Group	2	8.2	0.00
Social	Group	2	94.79	0.00
Vocal	Group	2	4.46	0.01
Other	Group	2	10.77	0.00

Appendix IV.

Tukey Pairwise Comparisons of the subsets (activity budget; age-sex class differences) (grouping information using the Tukey Method and 95% confidence) are listed below to show where the significant differences were between the subsets (sorted by the highest mean in descending order). Means that do not share a letter are significantly different.

Activity	**Subset**	**N**	**Mean**	**Grouping**		
Rest	Adult Female	156	50.33	A		
	Adult Male	168	48.11	A		
	Immature Individual	160	32.80		B	
Travel	Immature Individual	160	33.39	A		
	Adult Male	168	27.13		B	
	Adult Female	156	20.74			C
Feed	Adult Female	156	24.99	A		
	Immature Individual	160	20.95		B	
	Adult Male	168	19.70		B	
Social	Immature Individual	160	12.05	A		
	Adult Male	168	4.19		B	
	Adult Female	156	2.10			C
Vocal	Immature Individual	160	0.50	A		
	Adult Female	156	0.46	A		
	Adult Male	168	0.14		B	
Other	Adult Female	156	1.38	A		
	Adult Male	168	0.72		B	
	Immature Individual	160	0.30		B	

Appendix V.

The output of the general linear model (feeding time analysis); specifically, the analysis of variance. Displayed here are the degrees of freedom (DF), F-Value, and P-Value.

Food Type	**Source**	**DF**	**F-Value**	**P-Value**
Fruit	Sample Period	12	7.4	0.00
Leaf	Sample Period	12	3.38	0.00
Flower*	Sample Period	12	7.24	0.00
Other	Sample Period	12	3.66	0.00
Undetermined	Sample Period	12	3.23	0.00

Appendix VI.

Tukey Pairwise Comparisons of the sample periods (feeding time analysis) (grouping information using the Tukey Method and 95% confidence) are listed below to show where the significant differences were over the sample periods (sorted by the highest mean in descending order). Means that do not share a letter are significantly different.

Food Type	Sample Period	N	Mean	Grouping			
Fruit	Mar-03	47	59.87	A			
	Jun-03	29	49.57	A	B		
	Nov-03	27	47.80	A	B		
	Dec-03	15	45.44	A	B	C	
	May-03	29	45.32	A	B	C	
	Sep-03	35	38.60		B	C	
	Mar-04	35	38.09		B	C	
	Aug-03	29	35.35		B	C	D
	Jul-03	44	31.29		B	C	D
	Apr-03	40	29.93		B	C	D
	Jan-04	44	28.75		B	C	D
	Feb-04	42	25.33			C	D
	Oct-03	42	17.73				D
Leaf	Jul-03	44	53.82	A			
	Oct-03	42	50.57	A			
	Dec-03	15	49.50	A	B		
	Aug-03	29	49.17	A			
	Mar-04	35	49.14	A			
	Jan-04	44	47.35	A			
	Jun-03	29	44.96	A	B		
	Nov-03	27	43.98	A	B		
	Sep-03	35	42.79	A	B		
	Feb-04	42	42.32	A	B		
	Apr-03	40	39.16	A	B		
	May-03	29	32.85	A	B		
	Mar-03	47	25.67		B		
Flower*	Apr-03	40	30.65	A			
	Oct-03	42	29.46	A			
	Feb-04	42	23.86	A	B		
	May-03	29	20.50	A	B	C	D
	Jan-04	44	19.70	A	B	C	

	Mar-03	47	13.05		B	C	D
	Jul-03	44	11.86		B	C	D
	Sep-03	35	11.82		B	C	D
	Aug-03	29	10.08		B	C	D
	Nov-03	27	6.67			C	D
	Mar-04	35	6.04			C	D
	Jun-03	29	3.30				D
	Dec-03	15	1.22			C	D
Other	Sep-03	35	5.63	A			
	Aug-03	29	5.40	A	B		
	Mar-04	35	4.08	A	B	C	
	Feb-04	42	3.14	A	B	C	
	Jul-03	44	2.80	A	B	C	
	Jun-03	29	0.93	A	B	C	
	Mar-03	47	0.84		B	C	
	Oct-03	42	0.79		B	C	
	May-03	29	0.72	A	B	C	
	Jan-04	44	0.62		B	C	
	Apr-03	40	0.00			C	
	Dec-03	15	0.00	A	B	C	
	Nov-03	27	0.00		B	C	
Undetermined	Feb-04	42	5.35	A			
	Dec-03	15	3.84	A	B		
	Jan-04	44	3.58	A	B		
	Mar-04	35	2.65	A	B		
	Nov-03	27	1.55	A	B		
	Oct-03	42	1.46	A	B		
	Jun-03	29	1.24	A	B		
	Sep-03	35	1.17	A	B		
	May-03	29	0.61		B		
	Mar-03	47	0.58		B		
	Apr-03	40	0.26		B		
	Jul-03	44	0.24		B		
	Aug-03	29	0.00		B		

Appendix VII.

The output of the general linear model (feeding time analysis with maturity stated); specifically, the analysis of variance. Displayed here are the degrees of freedom (DF), F-Value, and P-Value.

Food Type	Source	DF	F-Value	P-Value
Mature Fruit	Sample Period	12	16.25	0.00
Immature Fruit	Sample Period	12	7.97	0.00
Fruit of Unknown Maturity	Sample Period	12	3.36	0.00
Mature Leaf	Sample Period	12	13.12	0.00
Immature Leaf	Sample Period	12	14.18	0.00
Leaf of Unknown Maturity	Sample Period	12	2.58	0.00
Flower	Sample Period	12	4.17	0.00
Bud	Sample Period	12	4.37	0.00
Stem	Sample Period	12	1.75	0.05
Bamboo	Sample Period	12	2.86	0.00
Nectar	Sample Period	12	15.23	0.00
Bark	Sample Period	12	3.35	0.00
Undetermined	Sample Period	12	3.23	0.00

Appendix VIII.

Tukey Pairwise Comparisons of the sample periods (feeding time analysis with maturity stated) (grouping information using the Tukey Method and 95% confidence) are listed below to show where the significant differences were over the sample periods (sorted by the highest mean in descending order). Means that do not share a letter are significantly different.

Food Type	**Sample Period**	**N**	**Mean**	**Grouping**				
Mature Fruit	Mar-03	47	46.50	A				
	Sep-03	35	23.81		B			
	Apr-03	40	21.79		B	C		
	May-03	29	19.14		B	C	D	
	Aug-03	29	15.87		B	C	D	E
	Jun-03	29	11.30		B	C	D	E
	Dec-03	15	10.68		B	C	D	E
	Nov-03	27	10.58		B	C	D	E
	Oct-03	42	8.52			C	D	E
	Jul-03	44	8.30			C	D	E
	Jan-04	44	5.03				D	E
	Mar-04	35	3.54				D	E
	Feb-04	42	2.97					E
Immature Fruit	Jun-03	29	38.27	A				
	Nov-03	27	37.22	A				
	Dec-03	15	34.76	A	B			
	Mar-04	35	34.27	A				
	May-03	29	25.97	A	B	C		
	Jan-04	44	23.73	A	B	C		
	Jul-03	44	22.80	A	B	C	D	
	Feb-04	42	22.20	A	B	C	D	
	Aug-03	29	19.43	A	B	C	D	
	Sep-03	35	14.61		B	C	D	
	Mar-03	47	11.03			C	D	
	Oct-03	42	9.21			C	D	
	Apr-03	40	7.87				D	
Fruit of Unknown Maturity	Mar-03	47	2.34	A				
	Mar-04	35	0.28		B			
	Apr-03	40	0.26		B			
	May-03	29	0.22		B			

	Jul-03	44	0.20		B			
	Sep-03	35	0.19		B			
	Feb-04	42	0.16		B			
	Aug-03	29	0.05		B			
	Jan-04	44	0.00		B			
	Oct-03	42	0.00		B			
	Dec-03	15	0.00		B			
	Nov-03	27	0.00		B			
	Jun-03	29	0.00		B			
Mature Leaf	Jul-03	44	51.13	A				
	Jun-03	29	42.96	A	B			
	Aug-03	29	39.93	A	B	C		
	Apr-03	40	28.85		B	C	D	
	Sep-03	35	28.52		B	C	D	
	May-03	29	27.45		B	C	D	E
	Mar-04	35	23.28			C	D	E
	Feb-04	42	18.68				D	E
	Oct-03	42	17.10				D	E
	Nov-03	27	11.84				D	E
	Mar-03	47	11.73					E
	Jan-04	44	11.35					E
	Dec-03	15	7.23				D	E
Immature Leaf	Dec-03	15	39.83	A				
	Jan-04	44	34.46	A				
	Oct-03	42	33.33	A				
	Nov-03	27	32.15	A				
	Mar-04	35	23.67	A	B			
	Feb-04	42	22.97	A	B			
	Sep-03	35	14.11		B	C		
	Mar-03	47	11.64		B	C		
	Aug-03	29	9.19		B	C		
	Apr-03	40	9.08		B	C		
	May-03	29	4.53			C		
	Jul-03	44	2.69			C		
	Jun-03	29	1.76			C		
Leaf of Unknown Maturity	Dec-03	15	2.45	A				
	Mar-03	47	2.30	A				
	Mar-04	35	2.19	A				
	Jan-04	44	1.54	A				
	Apr-03	40	1.23	A				
	May-03	29	0.87	A				

	Feb-04	42	0.67	A		
	Jun-03	29	0.23	A		
	Sep-03	35	0.15	A		
	Oct-03	42	0.13	A		
	Aug-03	29	0.06	A		
	Jul-03	44	0.00	A		
	Nov-03	27	0.00	A		
Flower	Feb-04	42	21.40	A		
	Oct-03	42	18.01	A	B	
	Jan-04	44	15.34	A	B	C
	Mar-03	47	11.30	A	B	C
	May-03	29	11.10	A	B	C
	Jul-03	44	10.73	A	B	C
	Aug-03	29	8.39	A	B	C
	Apr-03	40	8.12		B	C
	Nov-03	27	6.30		B	C
	Mar-04	35	3.60			C
	Sep-03	35	3.56			C
	Jun-03	29	2.05			C
	Dec-03	15	1.22		B	C
Bud	Oct-03	42	11.45	A		
	Sep-03	35	8.25	A	B	
	Apr-03	40	4.59	A	B	
	Jan-04	44	4.36		B	
	Feb-04	42	2.46		B	
	Mar-04	35	2.44		B	
	Mar-03	47	1.74		B	
	Aug-03	29	1.69		B	
	Jun-03	29	1.25		B	
	Jul-03	44	1.12		B	
	May-03	29	0.86		B	
	Nov-03	27	0.37		B	
	Dec-03	15	0.00		B	
Stem	Sep-03	35	2.97	A		
	Mar-04	35	2.04	A		
	Feb-04	42	1.14	A		
	Jul-03	44	1.01	A		
	Oct-03	42	0.79	A		
	May-03	29	0.72	A		
	Aug-03	29	0.71	A		
	Mar-03	47	0.51	A		
	Jan-04	44	0.16	A		

	Nov-03	27	0.00	A		
	Dec-03	15	0.00	A		
	Apr-03	40	0.00	A		
	Jun-03	29	0.00	A		
Bamboo	Feb-04	42	2.00	A		
	Mar-04	35	1.55	A	B	
	Jan-04	44	0.40	A	B	
	Mar-03	47	0.33	A	B	
	May-03	29	0.00		B	
	Aug-03	29	0.00		B	
	Sep-03	35	0.00		B	
	Dec-03	15	0.00	A	B	
	Jun-03	29	0.00		B	
	Jul-03	44	0.00		B	
	Oct-03	42	0.00		B	
	Nov-03	27	0.00		B	
	Apr-03	40	0.00		B	
Nectar	Apr-03	40	17.95	A		
	May-03	29	8.53		B	
	Mar-04	35	0.00			C
	Jan-04	44	0.00			C
	Sep-03	35	0.00			C
	Feb-04	42	0.00			C
	Aug-03	29	0.00			C
	Oct-03	42	0.00			C
	Dec-03	15	0.00		B	C
	Nov-03	27	0.00			C
	Jul-03	44	0.00			C
	Mar-03	47	0.00			C
	Jun-03	29	0.00			C
Bark	Aug-03	29	4.70	A		
	Sep-03	35	2.66	A	B	
	Jul-03	44	1.78	A	B	
	Jun-03	29	0.93	A	B	
	Mar-04	35	0.49		B	
	Jan-04	44	0.07		B	
	Apr-03	40	0.00		B	
	May-03	29	0.00		B	
	Feb-04	42	0.00		B	
	Mar-03	47	0.00		B	
	Oct-03	42	0.00		B	
	Dec-03	15	0.00		B	

	Nov-03	27	0.00		B
Undetermined	Feb-04	42	5.35	A	
	Dec-03	15	3.84	A	B
	Jan-04	44	3.58	A	B
	Mar-04	35	2.65	A	B
	Nov-03	27	1.55	A	B
	Oct-03	42	1.46	A	B
	Jun-03	29	1.24	A	B
	Sep-03	35	1.17	A	B
	May-03	29	0.61		B
	Mar-03	47	0.58		B
	Apr-03	40	0.26		B
	Jul-03	44	0.24		B
	Aug-03	29	0.00		B

Appendix IX.

The output of the general linear model (feeding time analysis; age-sex class differences); specifically, the analysis of variance. Displayed here are the degrees of freedom (DF), F-Value, and P-Value.

Food Type	**Source**	**DF**	**F-Value**	**P-Value**
Fruit	Group	2	0.00	0.99
Leaf	Group	2	0.00	0.99
Flower*	Group	2	0.03	0.96
Other	Group	2	0.28	0.75
Undetermined	Group	2	1.03	0.35

Appendix X.

Tukey Pairwise Comparisons of the groups (feeding time analysis; age-sex class differences) (grouping information using the Tukey Method and 95% confidence) are listed below to show where the significant differences were between the groups (sorted by the highest mean in descending order). Means that do not share a letter are significantly different.

Food Type	Group	N	Mean	Grouping
Fruit	Adult Female	152	38.11	A
	Adult Male	154	37.86	A
	Immature Individual	152	37.82	A
Leaf	Adult Female	152	44.02	A
	Adult Male	154	44.01	A
	Immature Individual	152	43.80	A
Flower*	Adult Male	154	14.83	A
	Adult Female	152	14.31	A
	Immature Individual	152	14.28	A
Other	Adult Male	154	2.11	A
	Immature Individual	152	2.04	A
	Adult Female	152	1.61	A
Undetermined	Immature Individual	152	2.06	A
	Adult Female	152	1.95	A
	Adult Male	154	1.19	A

Appendix XI.

The output of the general linear model (feeding time analysis with maturity stated; age-sex class differences); specifically, the analysis of variance. Displayed here are the degrees of freedom (DF), F-Value, and P-Value.

Food Type	Source	DF	F-Value	P-Value
Mature Fruit	Group	2	0.12	0.88
Immature Fruit	Group	2	0.09	0.91
Fruit of Unknown Maturity	Group	2	0.96	0.38
Mature Leaf	Group	2	0.68	0.50
Immature Leaf	Group	2	0.56	0.57
Leaf of Unknown Maturity	Group	2	0.68	0.50
Flower	Group	2	0.19	0.82
Bud	Group	2	0.10	0.90
Stem	Group	2	0.03	0.97
Bamboo	Group	2	0.88	0.41
Nectar	Group	2	0.32	0.72
Bark	Group	2	0.47	0.62
Undetermined	Group	2	1.03	0.35

Appendix XII.

Tukey Pairwise Comparisons of the groups (feeding time analysis with maturity stated; age-sex class differences) (grouping information using the Tukey Method and 95% confidence) are listed below to show where the significant differences were between the groups (sorted by the highest mean in descending order). Means that do not share a letter are significantly different.

Food Type	Group	N	Mean	Grouping
Mature Fruit	Adult Male	154	14.80	A
	Adult Female	152	14.78	A
	Immature Individual	152	13.82	A
Immature Fruit	Immature Individual	152	23.80	A
	Adult Male	154	22.91	A
	Adult Female	152	22.83	A
Fruit of Unknown Maturity	Adult Female	152	0.50	A
	Immature Individual	152	0.20	A
	Adult Male	154	0.15	A
Mature Leaf	Adult Male	154	25.77	A
	Adult Female	152	25.23	A
	Immature Individual	152	22.86	A
Immature Leaf	Immature Individual	152	19.88	A
	Adult Female	152	17.77	A
	Adult Male	154	17.60	A
Leaf of Unknown Maturity	Immature Individual	152	1.06	A
	Adult Female	152	1.02	A
	Adult Male	154	0.64	A
Flower	Adult Male	154	10.08	A
	Adult Female	152	9.02	A
	Immature Individual	152	8.85	A
Bud	Adult Female	152	3.42	A
	Adult Male	154	3.01	A
	Immature Individual	152	2.94	A
Stem	Adult Male	154	0.81	A
	Immature Individual	152	0.79	A
	Adult Female	152	0.71	A
Bamboo	Adult Male	154	0.53	A
	Adult Female	152	0.30	A

	Immature Individual	152	0.15	A
Nectar	Immature Individual	152	2.49	A
	Adult Female	152	1.87	A
	Adult Male	154	1.74	A
Bark	Immature Individual	152	1.09	A
	Adult Male	154	0.77	A
	Adult Female	152	0.59	A
Undetermined	Immature Individual	152	2.06	A
	Adult Female	152	1.95	A
	Adult Male	154	1.19	A