Feeding strategies to promote welfare and conservation of captive endangered primates

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2007/2008

A thesis submitted in partial fulfilment of the requirements for the degree of Master of Science and the Diploma of Imperial College London

Contents

1. Abstract

Appropriate nutrition is crucial for the health and well-being of captive primates. There is a need to address feeding practices to manage successfully, and propagate, primates of conservation concern. Improvement of feeding success can help to negate existing problems with diet composition and provisioning strategies that are still present for many captive primate species.

In this study, the feeding behaviour of three captive medium-sized primate species (black and white colobus *Colobus guereza kikuyuensis*, white-naped mangabey *Cercocebus atys lunulatus*, and red-faced black spider monkey *Ateles paniscus*) housed at ZSL London Zoo was assessed. The objective was to evaluate critically the current practices of nutritional management, from the perspective of animal behaviour and welfare.

Observations were recorded during feeding periods, and resulting data analysed statistically, to reveal the significance, or otherwise of the data, and consequences for feeding strategies. Unequal resource partitioning was not observed, as demonstrated by feeding durations of individuals not differing significantly. Also provisioned food was dispersed widely enough as to negate the occurrence of monopolisation. Disproportionate energetic gains, and any welfare implications which could potentially have resulted, are therefore unlikely.

The study is indicative that the feeding strategies utilised at ZSL London Zoo for these three captive primate species are effective. Application of these strategies should therefore contribute towards effective captive primate feeding in other institutions. Optimisation of captive primate health, well-being and welfare should then result, contributing to the improvement of breeding programmes. This has important and obvious advantages for primate species of conservation concern.

2. Introduction

Appropriate nutrition is crucial for the health and well-being of captive primates (Zinner, 1999; Addessi *et al.* 2005). Both dietary composition and the strategy of provisioning influence the physical and psychological fitness of an individual (Tovar *et al.* 2005). Optimising fitness is fundamental for species involved in captive breeding programmes (Edwards, 1997; Wielebnowski, 1998; Zinner, 1999), and it is particularly important to ensure that the management of species with a high conservation concern is evaluated (Boccia *et al.* 1988).

Captive animal nutrition has received a fair amount of scientific study; however, despite this, problems with diet composition and provisioning strategies still exist for many captive primate species (Schwitzer & Kaumanns, 2003). There is a shortage of research on what is considered 'good practice' for feeding captive primates. Many diets have developed through trial and error over many generations, as opposed to developing through the best evidence provided by applied research (Nijboer & Dierenfeld, 1996). There is clearly a need for increased research efforts on captive primate feeding.

A variety of scientific disciplines contribute to conservation, but only recently has behavioural ecology begun to address conservation issues (Caro, 1998; Møller & Danchin, 2008). The overall properties of populations, whether captive or otherwise, are determined by the properties of the individuals within these populations and the interactions occurring between them (Møller & Danchin, 2008). By taking into account the varying characteristics of individuals within populations, behavioural ecology provides an individual-based approach to conservation that other sciences cannot or do not provide (Møller & Danchin, 2008). Møller & Danchin (2008) state that the "ignorance of behavioural aspects of conservation may put overall conservation efforts at risk" (Møller & Danchin, 2008: p.663).

The aim of this study was to assess the feeding behaviour of three captive medium-sized primate species (BANR, 2003) (black and white colobus *Colobus guereza kikuyuensis*, white-naped mangabey *Cercocebus atys lunulatus*, and red-faced black spider monkey *Ateles paniscus*) housed at ZSL London Zoo, with regards to current dietary composition and provisioning strategies. The intention was to critically evaluate current nutritional management practices from the perspective of animal behaviour and welfare, and to make

recommendations if necessary. On a wider scale, it was hoped that the results of the study may contribute towards captive primate feeding in general, thus having an impact on ex situ conservation efforts of these species. The objectives were to determine if the provisioned diet was presented appropriately for the social structure of the group, and to investigate food access, preferences and feeding durations. Specific hypotheses which were tested are stated below.

Hypotheses

1. Access to food would not be equal between group members, with the dominant male approaching first and feeding first from the provisioned food.

2. The dominant male would remain in close proximity to the provisioned food whilst feeding, and thereafter proximity would follow the dominance hierarchy of the group.

3. Fresh food would be preferred over the dried pellet food that is known as 'monkey chow'.

4. The type of provisioned food consumed would not be equal between group members, with the dominant male consuming their preferred food type(s) thus leaving less choice for more subordinate individuals.

5. Food consumption would not be equal between group members, with the dominant male feeding for a longer duration.

3. Background

3.1 Background to current literature

Primate dominance and feeding patterns

Most groups of individuals in primate groups demonstrate dominance hierarchies (Chase *et al.* 2002). Primate dominance hierarchies are usually ascertained with regards to age (Manning & Stamp Dawkins, 1995; Emlen, 1997), with the older and therefore more experienced individuals dominant over the younger animals (Pusey & Packer, 1997). Exceptions do exist under varying circumstances, for example, very elderly or geriatric individuals are often subordinate (Pusey & Packer, 1997; Lintzenich & Ward, 2001), and female nepotism, commonly

seen in macaques *Macaca* also occurs, where a young female takes on the rank of her mother (Ridley, 1995). Male, as opposed to female dominance occurs in the majority of primate species (Radespiel & Zimmermann, 2001), with the 'alpha' male of a group being the most dominant.

The study of competition and the influence it can have on the fitness of individuals is an important issue where captive primate studies are concerned (Whitten, 1983). Behavioural consequences of competition include aggressive interactions, displacement (physical or otherwise) of an individual, or avoidance (Snaith & Chapman, 2007). Competition within groups for food can result in differential access to resources (Sterck & Steenbeek, 1997; Pruetz & Isbell, 2000; Stahl & Kaumanns, 2003; Snaith & Chapman, 2007). Dominant individuals are generally expected to have priority access to food, obtaining a larger proportion of the provisioned diet than subordinates (Janson, 1985; Belzung & Anderson, 1986; Manning & Stamp Dawkins, 1995; Pusey & Packer, 1997; Schwitzer & Kaumanns, 2003). Numerous studies have documented priority food access for dominant primates.

Dominant individuals have been observed gaining first access to the food (Boccia *et al.* 1988; Tovar *et al.* 2005). In captive rhesus monkeys *Macaca mulatta*, socially dominant group members tended to commence feeding before lower-ranking individuals (Brennan & Anderson, 1988). Similarly, Belzung & Anderson (1986) observed that dominant rhesus monkeys gained access to food faster than less dominant members of the group.

The total time an individual spends feeding can also be determined by dominance status (Janson, 1985; Belzung & Anderson, 1986). Dominant rhesus monkeys have been observed to feed for longer than subordinate individuals (Belzung & Anderson, 1986; Brennan & Anderson, 1988). Correlations between dominance rank and time feeding have also been documented in brown capuchin monkeys *Cebus apella* (Janson, 1985) and Japanese macaques *Macaca fuscata* (Saito, 1996).

Dominance rank has, in addition, been shown to influence overall individual food intake and energy acquisition (Barton & Whiten, 1993; Saito, 1996). Priority access to food has the potential to improve fitness of the individuals obtaining that priority (Whitten, 1983). However, conflicting research exists on whether dominance rank impacts to such a degree that overall food and energetic intake is affected, therefore compromising the welfare of subordinate individuals. Studies by both Janson (1985) and Barton & Whiten (1993) show

dominant individuals obtained significantly higher food intake than subordinate individuals and therefore experienced overall welfare benefits. Dominant brown capuchin monkeys attained 20.5% higher total energy intakes compared to subordinate individuals (Janson, 1985). In free-ranging female olive baboons *Papio anubis*, mean daily food intake of the most dominant individuals was found to be 30% greater than the intake of the subordinates (Barton & Whiten, 1993). In contrast, Deutsch & Lee (1991) observed no consistent differences in food intake between rhesus monkeys of different rank, despite dominant individuals having "greater access to feeding sites". The welfare of subordinate individuals in this instance was consequently not considered to be compromised.

Further research is required to determine the degree of influence dominance has upon differential food partitioning and subordinate individual welfare. Although a number of studies have taken place, with conflicting results it is possible that this issue varies species-specifically, and that food access and resulting welfare cannot be generalised for primates. Also, some of the above-mentioned research studied free-ranging primates. These may have limited value when comparing to captive studies, as captive primate groups often have relatively unnaturalistic social structures and environments. Food is guaranteed and readily available in zoos, and therefore group feeding may be more relaxed (Crissey, 2005). Conversely, limited space may promote higher levels of competition (SCAHAW, 2002).

Captive primate diets

In an attempt to ensure appropriate nutrition for captive primates, monkey chow, a high-energy pellet food designed to provide "a complete and balanced diet" is recommended (BANR, 2003; Addessi *et al.* 2005). This is usually presented alongside supplementary fruits, vegetables and seeds/ nuts, dependent upon the species concerned (BANR, 2003). However, primates do not consistently select a 'complete' diet when offered foods in captive situations (Oftedal & Allen, 1996), with individuals selecting the more appealing supplemented foods.

Although chow satisfies nutritional requirements, current literature has indicated that captive primates do not demonstrate an overwhelming desire to eat it (Addessi *et al.* 2005). Individual preferences can impact upon food consumption (Crissey, 2005). Tufted capuchin monkeys *Cebus apella* preferentially selected non-pellet foods when offered monkey chow or one of several fresh foods in laboratory-based two-alternative choice tests (Addessi *et al.*

2005). However, each individual was only able to select between two different foods (chow and one other) at any one time. The environment created was therefore artificial in comparison to how most primates held in zoos can make their feeding choices. Additionally, as individuals were alone when making their choices, social impacts were removed. Again, this differs from the usual zoo environment as social factors can also play a role in both individual and group feeding behaviour. Further research is therefore required to determine whether the findings of Addessi *et al.* (2005) are supported because, as far as is known, no other study has documented food selection preferences in captive primates.

Captive primate food provisioning strategies

An understanding of the social dominance characteristics affecting the feeding behaviour of a group is crucial when evaluating the management of captive primates (Blois-Heulin & Martinez- Cruz, 2005). If the diet is presented inappropriately for the social structure of the group, there is potential for suboptimal welfare, either in relation to nutritional deficiencies in individuals or to resultant injuries from food competition (Whitten, 1983).

If food is distributed in a way which allows it to be monopolised, for some individuals a larger proportion of the provisioned diet and therefore biased energy gains may result (Sterck & Steenbeek, 1997; Pruetz & Isbell, 2000; Stahl & Kaumanns, 2003; Snaith & Chapman, 2007). Those who monopolise resources tend to be the more dominant individuals (Manning & Stamp Dawkins, 1995; Blois- Heulin & Martinez- Cruz, 2005). Monopolisation of resources has been documented for adult male red-capped mangabeys *Cercocebus torquatus torquatus* and grey-cheeked mangabeys *Lophocebus albigena* (Blois- Heulin & Martinez- Cruz, 2005), bonnet macaques *Macaca radiata* (Boccia *et al.* 1988) and female vervet monkeys *Cercopithecus aethiops* (Whitten, 1983).

If provisioned food cannot be easily accessed by each individual, nutrient intake may be compromised (Crissey, 2005). It is therefore expected that food acquisition may be more equal between group members when food is provisioned across a larger area (Michels, 1998). Dispersing food more widely increases the opportunity for each individual to access the food (Crissey, 2005), and also has been seen to reduce within-group aggression whilst feeding (Saito, 1996; Sterck & Steenbeek, 1997; Blois- Heulin & Martinez- Cruz, 2005). Negative social interactions were seen to decrease significantly in the earlier mentioned mangabey study when food was

presented in multiple piles as opposed to one pile (Blois- Heulin & Martinez- Cruz, 2005). Similar results were obtained by Boccia *et al.* (1988), Brennan & Anderson (1998) and Saito (1996) for bonnet macaques, rhesus monkeys and female Japanese macaques, respectively. As well as reducing within-group aggression, dispersed provisioning increases the likelihood of the earlier mentioned more equal food acquisition (Blois- Heulin & Martinez- Cruz, 2005).

Variation in access and food acquisition between group members only appears to occur significantly when food is provisioned in clumps as opposed to being more widely dispersed. Stahl & Kaumanns (2003) showed that for captive female sooty mangabeys *Cercocebus torquatus atys*, access to food was only rank-dependent when food was provided clumped. In free-ranging female vervet monkeys, variation in intake only occurred with respect to dominance rank when resources were clumped (Whitten, 1983). Similar patterns were also obtained in free-ranging Japanese macaques *Macaca fuscata yakui* (Furuichi, 1983). As demonstrated, a large body of research exists detailing the issues resulting from the clumped distribution of food. Therefore, it should be ensured food is distributed widely enough to reduce, as far as possible, the monopolisation of food and unequal resource partitioning within captive primate groups. However, there exists no clear, specific statement of an exact method for food provisioning, including what constitutes food being dispersed, to allow more equitable access for individuals of captive primate groups.

Existing advice available on the feeding behaviour of primates in captivity can be seen to be rather general (Edwards, 1997), and findings obtained from studies of feeding behaviour appear not to have been linked to direct application. As far as is known, no definitions or specifications exist as to what constitutes correct and appropriate provisioning strategies, or no indications of particular procedures that should be followed for feeding captive primates. Instead, general indications of potential issues resulting are available, and therefore more what practices to avoid (See: Whitten, 1983; Stahl & Kaumanns, 2003; Crissey, 2005; Snaith & Chapman, 2007). Additionally, primate feeding behaviour studies, although carried out using captive groups, are also conducted for free-ranging individuals. Though useful for obtaining information, the application of the findings of latter studies may not necessarily be representative for captive feeding practices.

Summary of captive primate nutrition

It has been ascertained that the composition of the provisioned diet (Addessi *et al.* 2005; Crissey, 2005), the manner of food presentation (Sterck & Steenbeek, 1997; Zinner, 1999; Pruetz & Isbell, 2000; Stahl & Kaumanns, 2003; Snaith & Chapman, 2007) and the social interactions occurring between group members can all impact upon feeding behaviour in captive primates (Boccia *et al.* 1988; Manning & Stamp Dawkins, 1995; Brennan & Anderson, 1998; Blois- Heulin & Martinez- Cruz, 2005). Further research, especially obtained from captive groups under natural zoo feeding conditions is required. Contributions should therefore be made to issues that still exist regarding diet composition and provisioning strategies for many captive primates (Nijboer & Dierenfeld, 1996; BANR, 2003; Schwitzer & Kaumanns, 2003). Effectiveness of captive breeding may therefore be improved, having important benefits for primate species of conservation concern (Edwards, 1997; Wielebnowski, 1998; Zinner, 1999; Wharton, 2007).

3.2 Introduction to study species

This study investigates the feeding behaviour of captive black and white colobus *Colobus guereza kikuyuensis*, white-naped mangabey *Cercocebus atys lunulatus*, and red-faced black spider monkey *Ateles paniscus* groups.

The black and white colobus is classified on the IUCN Red List as Lower Risk Least Concern (IUCN, 2007) and of the colobine species, is one of the most commonly represented in captivity (ILAR, 1998). However, colobine monkeys overall are less frequently found in captivity, primarily due to problems with developing an appropriate diet for them (ILAR, 1998). In the wild, this particular colobus species is found in central Kenya (Gron, 2007a), living in small groups composing one adult male, several adult females, and immature individuals (Björnsdotter *et al.* 2000; Gron, 2007b). However, multi-male groups are common (BANR, 2003; Gron, 2007b). Colobus monkeys possess multi-chambered stomachs with microbes in the foregut, allowing for plant fibre digestion (Tovar *et al.* 2005). They are therefore capable of consuming large quantities of leaf material (Edwards, 1997; Björnsdotter *et al.* 2000; BANR, 2003), and resultantly devote extended periods of time to resting to allow digestion (Björnsdotter *et al.* 2000; Schwitzer & Kaumanns, 2003; Gron, 2007a).

The white-naped mangabey is classified on the IUCN Red List as Critically Endangered under criteria A2cd (IUCN, 2007), due to a number of factors including habitat

loss and degradation, and harvesting for food i.e. bushmeat (IUCN, 2007). Only ~fifty individuals are found in captive breeding centres worldwide (WAPCA, 2008; Wolters, 2008). In the wild, this species is restricted to small forest patches in Ghana and the Côte d'Ivoire (McGraw *et al.* 2005; IUCN, 2007), living in larger multi-male, multi-female groups (BANR, 2003; McGraw *et al.* 2005).

The red-faced black spider monkey is classified on the IUCN Red List as Least Concern (IUCN, 2007). In the wild, this particular species is found in eastern South America (Cawthon Lang, 2007), commonly living in mixed sex groups of 3-35 individuals (BANR, 2003). Spider monkeys display a high degree of frugivory (Laska *et al.* 2000; BANR, 2003).

4. Methods

4.1 Study species

The study was conducted on three captive primate species housed at ZSL London Zoo, U.K. Each species was represented by a separately housed group. Details of each species are given in Table 1.

Table 1. Details of study species. * Subjects were identified by a single letter

Species	*Group composition*	*Males: ID* and age*	*Females: ID* and age*	Notes
Black and white colobus (*Colobus guereza kikuyuensis)*	2.2	1. R (8 yrs) 2. F (6 yrs)	1. N (4 yrs) 2. S (4 yrs)	Male F is castrated
White-naped mangabey (*Cercocebus atys lunulatus)*	1.2	1. LU (6 yrs)	1. LE (6yrs) 2. B (5yrs)	Female B had newborn infant
Red-faced spider monkey (*Ateles paniscus)*	1.2 (+1)	1. B (10 yrs)	1. C (17 yrs) 2. P (~37 yrs)	Additional individual, S, (2 yrs) of unknown sex

4.2 Feeding regimes

All species were fed twice daily, in the morning (between 9.00am-10.30am) and late afternoon (between 4.30pm-6.00pm). Both fresh food and monkey chow (Mazuri Primate Diet, Special Diets Services Ltd., Essex) were provided at these times (see Appendix 2 for more detailed feeding schedules). Food was provisioned in clumps, with several food clumps widely distributed across the enclosure. For the colobus and spider monkey groups, food was provisioned in the indoor section of the enclosure. For the mangabey group, food was distributed either indoors or outdoors (varying by day, dependent on keeping staff).

Groups had access to all parts of their enclosures during the day. Exceptions were when enclosures were being cleaned (between 8.30am-10.30am), when food was being distributed, and when the oldest female of the spider monkey group was separated for a short period (~15 minutes) during morning and late afternoon feeds. This allowed the female greater opportunities to access food, as keepers had previously noticed that she found it difficult to access food when the rest of the group was present (T. Lee, pers. comm.).

4.3 Procedures

4.3.1 Pilot study

A pilot study was conducted from 7th- 9th May 2008. Each species was observed, utilising ad libitum sampling (Altman, 1974; Martin & Bateson, 1993; BANR, 2003) at random time periods, both during and outside of feeding times. The pilot study allowed selection of the most appropriate sampling and recording methods and intervals, construction of ethograms and data recording sheets, and provided an opportunity to learn to distinguish between individuals in each group (Martin & Bateson, 1993). The pilot study also highlighted differences in the spider monkey group regarding separation at feeding times, and adjustments regarding data collection for this species could be arranged (as detailed below).

4.3.2 Behavioural observation schedule

Data collection took place between 12th May- 12th June 2008, on a total of 24 days (including weekdays, weekends and over one bank holiday weekend), totaling ~85 hours of observations. Between one and six hours of observations were undertaken each day.

Observations were randomised for group, day and time of day, and only one group was observed at a time. Groups were observed in both the indoor and outdoor sections of their enclosures, apart from the spider monkey group as it was not possible for the observer to move between the indoor and outdoor viewing areas during an observational period. All observed behaviours are defined in the ethogram (see Appendix 3).

4.3.3 Observation of non-feeding periods

Each observation period (randomised for group, day and time of day) consisted of one hour of observation. Focal sampling at five minute intervals was utilised to collect behavioural data (Altman, 1974; Martin & Bateson, 1993). Non-feeding periods took place outside of feeding times, either in the morning or afternoon, and data recording commenced when the stopwatch was started (designated as time 0).

A single focal individual was selected at random and its behaviour recorded using instantaneous sampling of state behaviours at five minute intervals, commencing from time 0. If food was being consumed the type was noted (see Appendix 1). Each group member was observed as a focal individual for a minimum of four separate observation periods over the entire course of the study.

Additionally, all aggressive interactions (event behaviours) (see ethogram, Appendix 3) were recorded from time 0 utilising all-occurrence sampling (Altman, 1974; Boccia *et al.* 1988; Brennan & Anderson, 1988; Martin & Bateson, 1993; BANR, 2003), detailing the initiator and receiver in each interaction. This allowed data to be obtained giving true measures of aggression; discrete events which would otherwise be missed using instantaneous sampling alone (Martin & Bateson, 1993).

4.3.4 Observation of feeding periods

Each observation period (randomised for group, day and time of day) consisted of one hour of observation. Instantaneous scan sampling of state behaviours at one minute intervals was utilised (Altman, 1974; Belzung & Anderson, 1986; Brennan & Anderson, 1988; Deutsch & Lee, 1991; Martin & Bateson, 1993; BANR, 2003; Blois- Heulin & Martinez- Cruz, 2005). This allowed data to be obtained that was evenly representative across individuals, and within and

between days, as opposed to with using focal sampling during feeding periods (Martin & Bateson, 1993).

Data recording commenced when food had been distributed by keeping staff, and the dividing door preventing access to the entire enclosure was re-opened (designated as time 0, timed on stopwatch). The first individual to approach the food and the first to commence feeding were recorded, as were the times at which these took place. Groups were scanned every minute, commencing from time 0, to record the instantaneous behaviour of each individual. If food was being consumed the type was noted, as was the proximity of each individual with regards to the food, either feeding at, less than two metres from, or greater than two metres from the food provisioned (judged by sight).

Each group was observed during a minimum of nine feeding observation periods over the entire course of the study. Additionally for the spider monkey group, all aggressive interactions were recorded from time 0 utilising all-occurrence sampling (Altman, 1974; Boccia *et al.* 1988; Brennan & Anderson, 1988; Martin & Bateson, 1993), detailing the initiator and receiver of each interaction. Additional sampling of aggressive interactions took place for this species due to the group's unique food provisioning practice, meaning data of a slightly different nature had to be collected.

4.4 Data analysis

4.4.1 Determination of dominance hierarchies and feeding activity

Baseline dominance hierarchies were determined for each group utilising the numbers of aggressive interactions observed during non-feeding periods. Aggressive interactions recorded in the spider monkey group during feeding periods were analysed separately. Hierarchies were determined for female-female and male-male dyads separately, within each group. The youngest member of the spider monkey group, S, was omitted from dominance analyses as the sex of the individual was unknown (P. Kybett, pers. comm.). The number of aggressive interactions between pairs were summed then presented in a matrix (Zumpe & Michael, 1986; Martin & Bateson, 1993). Each matrix was rearranged so the individual initiating most aggressive interactions was at the top, and the individual initiating the fewest aggressive interactions was at the bottom of the matrix (Martin & Bateson, 1993). As there were

never more than two individuals per matrix, calculation of Landau's index of linearity (Landau, 1951) was not required as complete linearity was assumed (Singh et al. 2003). Following construction of the matrices, each individual within was assigned a rank order (ordinal), indicating dominance status (Zumpe & Michael, 1986; Singh et al. 2003).

4.4.2 Statistical analysis

Normality of data was checked using Anderson-Darling Normality tests, and log-transformed if necessary (Townend, 2005). Data was analysed using one-way ANOVA, and two-sample and paired t-tests, and for non-normally distributed data or count data, using Kruskal-Wallis, Mann-Whitney U, two-sample sign and chi-square tests. Statistical significance for all analyses was determined at $P \leq 0.05$. Where appropriate, data are presented as mean ± Standard Deviations (S.D.) or as counts, and all analyses were carried out using the statistical package Minitab (version 15.0).

5. Results

Results shall be presented for black and white colobus, white-naped mangabey and red-faced black spider monkey groups in turn.

5.1 Black and white colobus

5.1.1 Dominance hierarchies

From the summed aggressive interactions for same-sex dyads in Table 2, it can be observed that the dominant male from the colobus group is individual R, and the dominant female, individual N.

Table 2. Aggressive interactions for same-sex dyads for the colobus group summed from non-feeding observations. Arrows indicate the direction of the interaction between individuals from initiator to receiver.

Direction of interactions	Number of interactions
Males: R → F	15
F → R	0
Females: N → S	57
S → N	34

From hereafter, the rank of individuals within each group will be labelled as follows: (DM)= dominant male, (SM)= subordinate male, (DF)= dominant female and (SF)= subordinate female.

5.1.2 Food access

The percentage of observations where each individual in the colobus group was first to arrive at the provisioned food (shaded bars) and first to commence feeding (unshaded bars) across the entire study period can be observed in Figure 1. Individual S, the subordinate female did not arrive at the food first, or commence feeding first on any occasion.
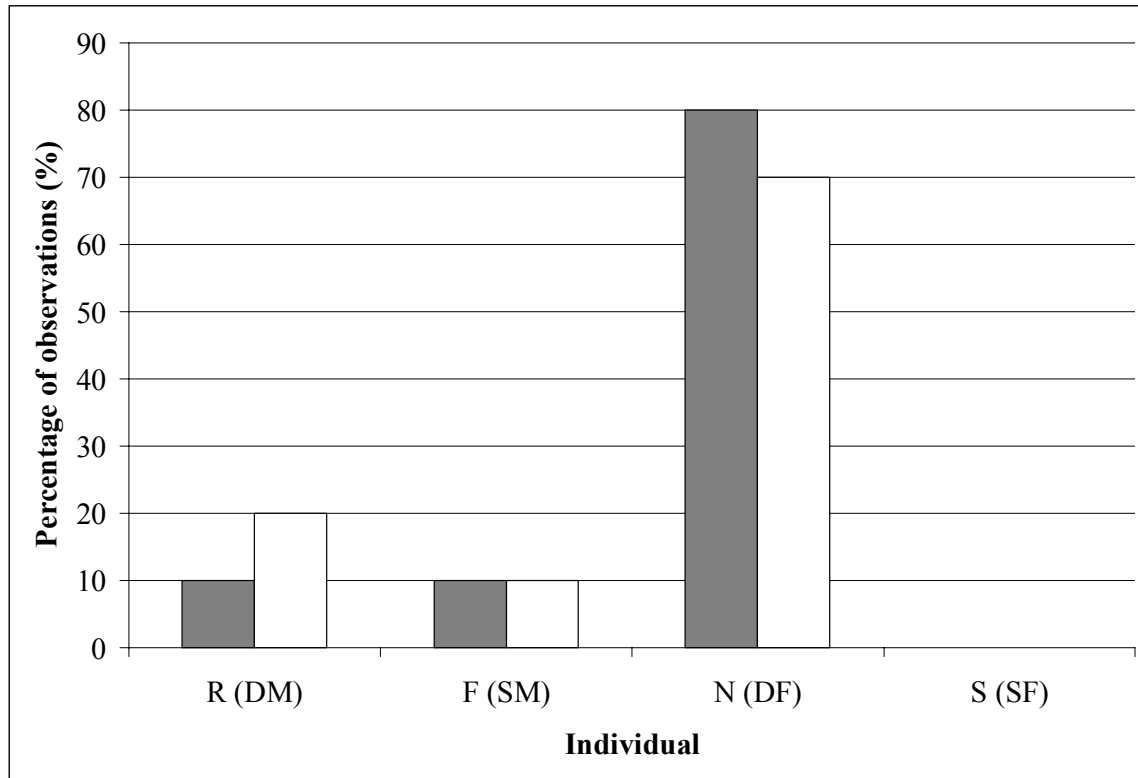
Figure 1. Total percentage of observations (%) each individual was first to arrive at the provisioned food (denoted by shaded bars) and first to commence feeding (denoted by un-shaded bars) for the colobus group across the entire study period.

The dominant female arrived first at the provisioned food and was first to commence feeding most frequently during the study period (Figure 1.).

The total number of scans each individual from the colobus group was observed feeding either (a) at the provisioned food, (b) less than two metres from the provisioned food and (c) greater than two metres from the provisioned food can be observed in Table 3. Values include data summed from all feeding observation periods across the entire study.

Table 3. Total number of scans each individual was observed feeding either at, less than 2m from or greater than 2m from the provisioned food for the colobus group across the entire study period. The values in brackets represent the percentage of scans that the food was consumed by that individual for each proximity.

Individual	Proximity to provisioned food		
	At	Less than 2m from	Greater than 2m from
R (DM)	98 (72.06)	21 (15.44)	17 (12.5)
F (SM)	78 (64.46)	19 (15.7)	24 (19.84)
N (DF)	75 (60.98)	30 (24.39)	18 (14.63)
S (SF)	52 (68.42)	13 (17.11)	11 (14.47)

The total number of scans engaged in feeding at the three measured distances differed significantly for each member of the colobus group (Chi-square tests: DM χ^2=91.96, P<0.001, df=2; SM χ^2=53.07, P<0.001, df=2; DF χ^2=44.05, P<0.001, df= 2; SF χ^2=42.18, P<0.001, df= 2). All individuals fed preferentially at the provisioned food (Table 3.), though there were significant differences in the total number of scans between individuals (Chi-square test: χ^2=14.06, P<0.01, df=3). The dominant male spent more time in close proximity to the food (i.e. at the provisioned food) compared to the rest of the group, and the subordinate female spent less time.

5.1.3 Food preferences

The mean time (minutes) spent feeding on fresh food differed significantly from the mean time spent consuming monkey chow for all individuals within the colobus group (Figure 2.). (Two-sample sign tests: DM Median=-14.50, P<0.01; SM Median=-12.50, P<0.01; DF Median=-11.00, P<0.01; SF Median=-10.50, P<0.01). Only the dominant female ate monkey chow during observations.
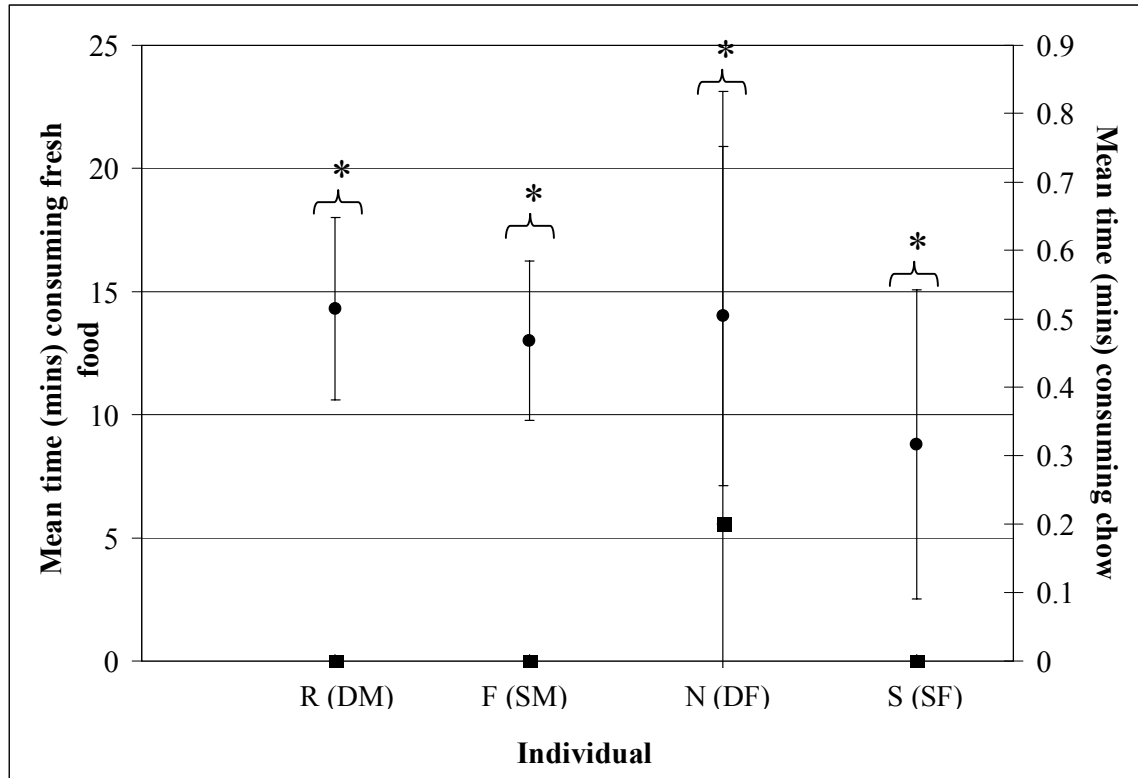
Figure 2. Mean time spent engaged in consumption of monkey chow (denoted by ■) and fresh food (denoted by ●) during observations of feeding periods by individuals of the colobus group. The error bars represent ± 1 S.D. Bracketed values indicate significant differences between monkey chow and fresh food at *P<0.01.

The total number of scans each individual from the colobus group was observed feeding on each fresh food type can be observed in Table 4. Values represent data summed from all feeding observation periods across the entire study. For definitions of food types, see Appendix 1.

Table 4. Total number of scans each individual was observed feeding on each fresh food type for the colobus group across the entire study period. The values in brackets represent the percentage of scans that the food type was consumed by that individual.

Individual	Fresh food type			
	Vegetables	Leafy greens	Enclosure vegetation	Other
R (DM)	59 (41.26)	20 (13.99)	7 (4.89)	57 (39.86)
F (SM)	51 (39.23)	26 (20.00)	9 (6.92)	44 (33.85)
N (DF)	30 (21.58)	31 (22.30)	19 (13.67)	59 (42.45)
S (SF)	13 (14.77)	12 (13.64)	18 (20.45)	45 (51.14)

The total number of scans observed feeding on each fresh food type differed significantly for each member of the colobus group (Chi-square tests: DM χ^2=57.81, P<0.001, df=3; SM χ^2=32.89, P<0.001, df=3; DF χ^2=25.12, P<0.001, df=3; SF χ^2=33.00, P<0.001, df=3). Both dominant and subordinate males showed preferences for 'Vegetables' and 'Other', though the total number of scans observed feeding on either of these did not differ significantly between the individuals (Chi-square tests: Vegetables χ^2=0.58, P=0.446, df=1; Other χ^2=1.67, P=0.196, df=1). Both dominant and subordinate females showed preferences only for 'Other', though the total number of scans observed feeding on this food type did not differ significantly between the individuals (Chi-square test: χ^2=1.88, P=0.17, df=1).

5.1.4 Feeding durations

A Kruskal-Wallis test indicated that there was no significant difference between individuals in the mean time spent feeding on fresh food and chow combined (H=5.09, P=0.166, df=3). Comparisons within same-sex dyads indicated that there was no significant difference in time spent feeding (fresh food and monkey chow combined) (Paired t-test, males: T=0.85, P=0.419, Two-sample sign test, females: Median=-4.00, P=0.1094). However, in both males and females, the dominant animal spent a longer mean time engaged in consumption of fresh food than the subordinate animal (Figure 2.), though this did not

differ significantly within either same-sex dyad (Paired t-test, males: T=0.85, P=0.419, Two-sample sign test, females: Median=-4.00, P=0.1094).

5.2 White-naped mangabey

5.2.1 Dominance hierarchies

From the summed aggressive interactions for same-sex dyads in Table 5, it can be observed that the dominant female from the mangabey group is individual LE.

Table 5. Aggressive interactions for same-sex dyads for the mangabey group summed from non-feeding observations. Arrows indicate the direction of the interaction between individuals from initiator to receiver.

Direction of interactions	Number of interactions
Females: LE → B B → LE	 12 1

5.2.2 Food access

The percentage of observations where each individual in the mangabey group was first to arrive at the provisioned food (shaded bars) and first to commence feeding (unshaded bars) across the entire study period can be observed in Figure 3. Individual LE, the dominant female did not arrive at the food first, or commence feeding first on any occasion.
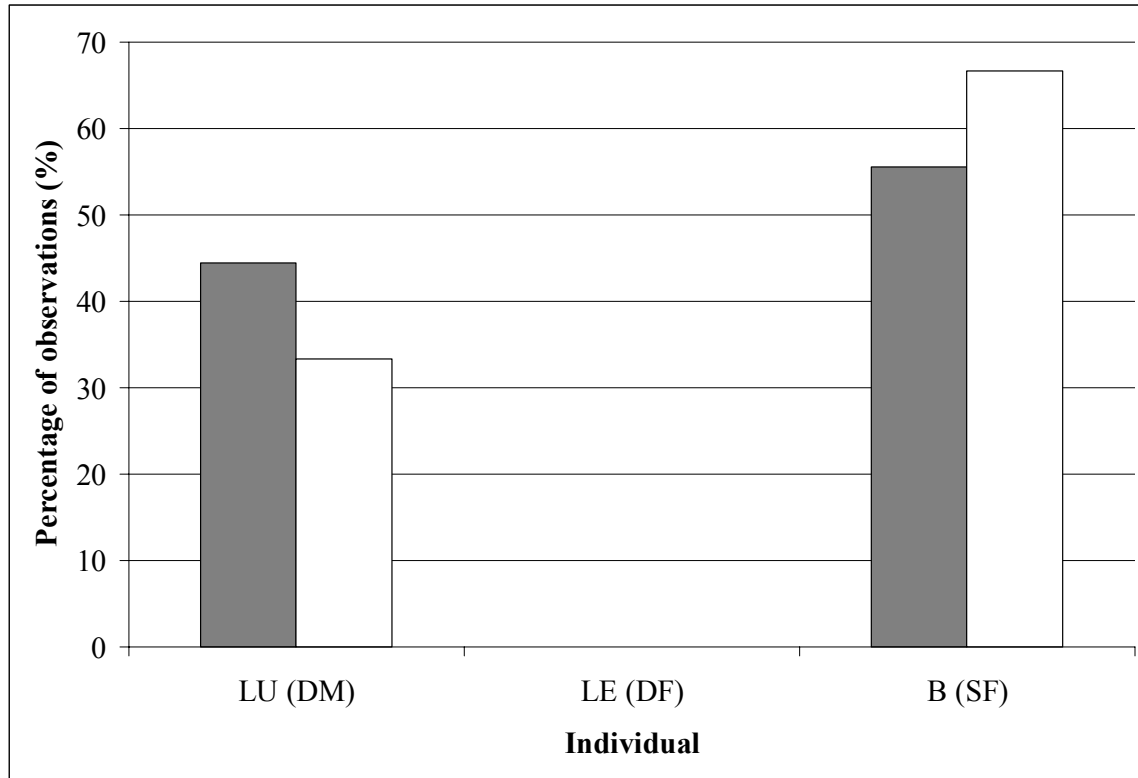
Figure 3. Total percentage of observations (%) each individual was first to arrive at the provisioned food (denoted by shaded bars) and first to commence feeding (denoted by un-shaded bars) for the mangabey group across the entire study period.

The subordinate female arrived first at the provisioned food and was first to commence feeding most frequently during the study period, though the dominant male also obtained first access and fed first (Figure 3.).

The total number of scans each individual from the mangabey group was observed feeding either (a) at the provisioned food, (b) less than two metres from the provisioned food and (c) greater than two metres from the provisioned food can be observed in Table 6. Values include data summed from all feeding observation periods across the entire study.

Table 6. Total number of scans each individual was observed feeding either at, less than 2m from or greater than 2m from the provisioned food for the mangabey group across the entire study period. The values in brackets represent the percentage of scans that the food was consumed by that individual for each proximity.

	Proximity to provisioned food		
Individual	**At**	**Less than 2m from**	**Greater than 2m from**
LU (DM)	38 (60.32)	11 (17.46)	14 (22.22)
LE (DF)	11 (16.18)	19 (27.94)	38 (55.88)
B (SF)	34 (41.46)	25 (30.49)	23 (28.05)

The total number of scans engaged in feeding at the three measured distances differed significantly for two members of the mangabey group (Chi-square tests: DM χ^2=20.86, P<0.001, df=2; DF χ^2=16.97, P<0.001, df=2). The subordinate female did not show a significant difference in the total number of scans engaged in feeding at the three measured distances (Chi-square test: SF χ^2=2.51, P=0.285, df=2). The dominant male fed preferentially at the provisioned food, whilst the dominant female fed preferentially greater than two metres from. The subordinate female showed no significant preference (Table 6.). There were significant differences in the total number of scans between individuals, with the dominant male and the subordinate female spending more time in close proximity to the food (at the provisioned food) compared to the dominant female, who spent less time (Chi-square test: χ^2=15.35, P<0.001, df=2).

5.2.3 Food preferences

The mean time (minutes) spent feeding on fresh food differed significantly from the mean time spent consuming monkey chow for all individuals within the mangabey group (Figure 4.). (Two-sample sign tests: DM Median=-19.00, P<0.01; DF Median=-20.00, P<0.01; SF Median=-12.00, P<0.01). The dominant female was the only individual not to feed on monkey chow during observations.
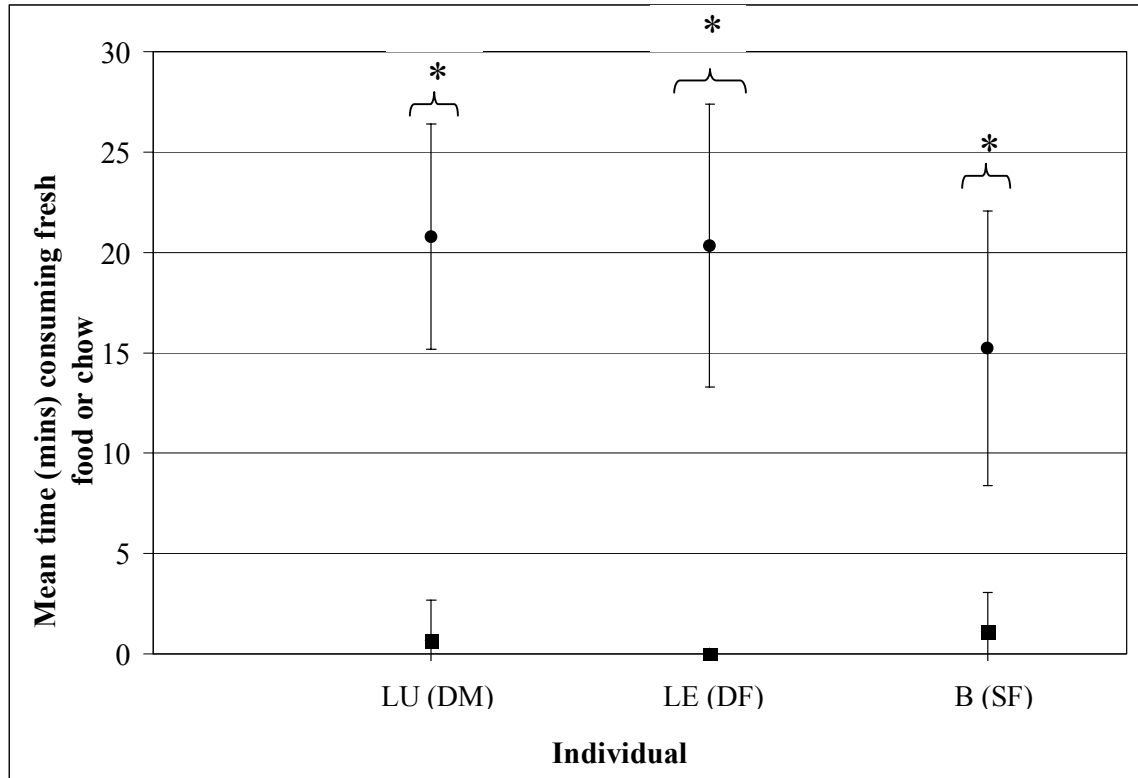
Figure 4. Mean time spent engaged in consumption of monkey chow (denoted by ■) and fresh food (denoted by ●) during observations of feeding periods by individuals of the mangabey group. The error bars represent ± 1 S.D. Bracketed values indicate significant differences at *P<0.01.

The total number of scans each individual from the mangabey group was observed feeding on each fresh food type can be observed in Table 7. Values represent data summed from all feeding observation periods across the entire study. For definitions of food types, see Appendix 1.

Table 7. Total number of scans each individual was observed feeding on each fresh food type for the mangabey group across the entire study period. The values in brackets represent the percentage of scans that the food type was consumed by that individual.

Individual	Fresh food type				
	Vegetables	Leafy greens	Fruit	Enclosure vegetation	Other
LU (DM)	33 (17.65)	1 (0.53)	23 (12.30)	16 (8.56)	114 (60.96)
LE (SM)	33 (18.03)	3 (1.64)	32 (17.49)	42 (22.95)	73 (39.89)
B (SF)	42 (30.66)	0 (0.00)	30 (21.89)	16 (11.68)	49 (35.77)

The total number of scans observed feeding on each fresh food type differed significantly for each member of the mangabey group (Chi-square tests: DM χ^2=210.62, P<0.001, df=4; DF χ^2=68.78, P<0.001, df=4; SF χ^2=57.20, P<0.001, df=4). Both the dominant male and female showed preferences for 'Other' and the subordinate female for 'Vegetables' and 'Other'. The total number of scans observed feeding between the dominant and subordinate females did not differ significantly for 'Vegetables' (Chi-square test: χ^2=1.08, P=0.299, df=1) but did differ significantly for 'Other' (Chi-square test: χ^2=4.72, P<0.05, df=1) (Table 7.) All individuals showed minimal interest in 'Leafy greens'.

5.2.4 Feeding durations

A one-way ANOVA indicated that there was no significant difference between individuals in the mean time spent feeding on fresh food and chow combined (r^2=3.94%, P=0.236, df=2). Comparisons within same-sex dyads indicated that there was no significant difference in time spent feeding (fresh food and monkey chow combined) (Paired t-test, females: T=-1.23, P=0.255). However, the more dominant female spent a longer mean time engaged in consumption of fresh food than the more subordinate animal (Figure 4.), though this did not differ significantly within the female dyad (Paired t-test: Median=-1.52, P=0.168).

5.3 Red-faced black spider monkey

5.3.1 Dominance hierarchies

From the summed aggressive interactions for same-sex dyads in Table 8, it can be observed that the dominant female from the spider monkey group is individual C.

Table 8. Aggressive interactions for same-sex dyads for the spider monkey group summed from non-feeding observations. Arrows indicate the direction of the interaction between individuals from initiator to receiver.

Direction of interactions	Number of interactions
Females: C → P	9
P → C	0

From hereafter, the rank of individuals will be labelled as set out in section 5.1.1, apart from the juvenile of undetermined sex from the spider monkey group who will be identified by (U).

5.3.2 Food preferences

The mean time (minutes) spent feeding on fresh food differed significantly from the mean time spent consuming monkey chow for three individuals within the spider monkey group (Figure 5.) (Two-sample sign tests: DM Median=-7.00, $P<0.01$; DF Median=-7.00, $P<0.01$; U Median=-3.00, $P<0.01$) but not significantly for the remaining individual of the group (Two-sample sign test: SF Median=00.00, $P=0.25$). Only individual B, the dominant male of the group ate monkey chow during the observations.
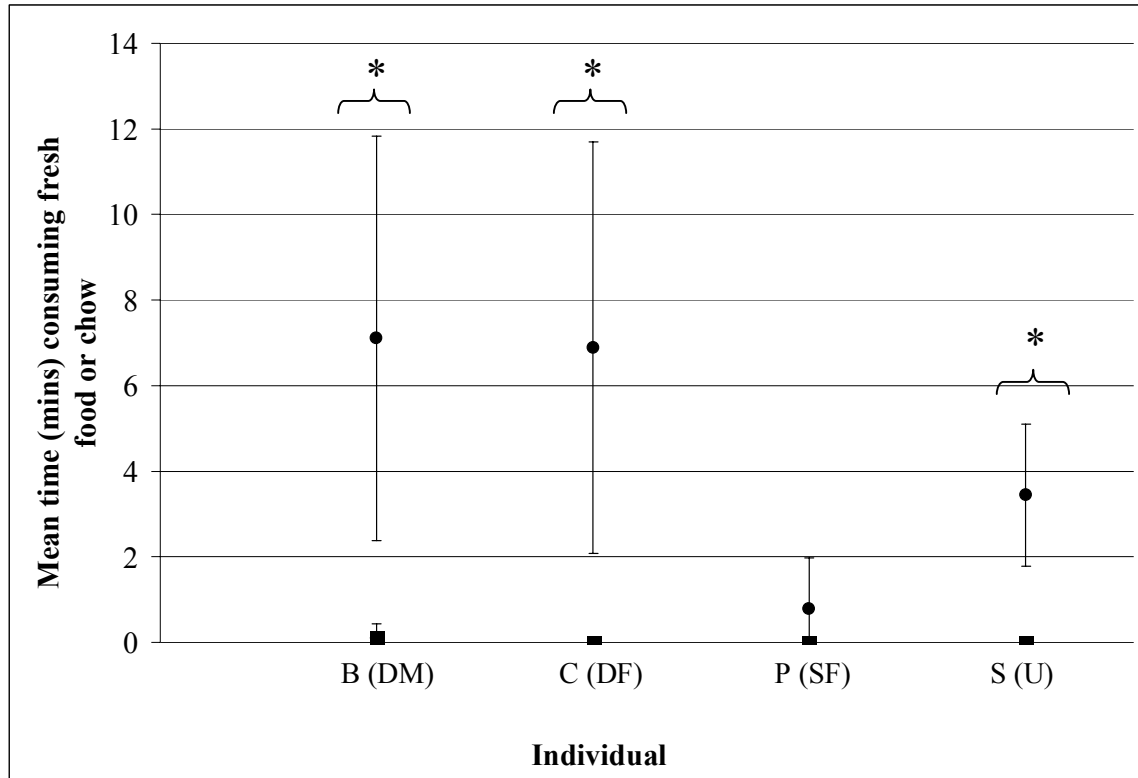
Figure 5. Mean time spent engaged in consumption of monkey chow (denoted by ■) and fresh food (denoted by ●) during observations of feeding periods by individuals of the spider monkey group. The error bars represent ± 1 S.D. Bracketed values indicate significant differences at *P<0.01.

The total number of scans each individual from the spider monkey group was observed feeding on each fresh food type can be observed in Table 9. Values represent data summed from all feeding observation periods across the entire study. For definitions of food types, see Appendix 1.

Table 9. Total number of scans each individual was observed feeding on each fresh food type for the spider monkey group across the entire study period. The values in brackets represent the percentage of scans that the food type was consumed by that individual.

	Fresh food type				
Individual	Vegetables	Leafy greens	Fruit	Enclosure vegetation	Other
B (DM)	9 (14.06)	12 (18.75)	17 (26.56)	0 (0.00)	26 (40.63)
C (DF)	6 (9.68)	9 (14.51)	20 (32.26)	0 (0.00)	27 (43.55)
P (SF)	0 (0.00)	2 (28.57)	0 (0.00)	0 (0.00)	5 (71.43)
S (U)	6 (19.36)	2 (6.45)	14 (45.16)	0 (0.00)	9 (29.03)

The total number of scans observed feeding on each fresh food type differed significantly for each member of the spider monkey group (Chi-square tests: DM χ^2=28.97, P<0.001, df=4; DF χ^2=38.48, P<0.001, df=4; SF χ^2=13.71, P<0.01, df=4; U χ^2=20.13, P<0.001, df=4). Both the dominant male and female showed preferences for 'Fruit' and 'Other', the subordinate female for 'Other', and the unknown individual showed a preference for 'Fruit'. The total number of scans observed feeding differed significantly between the dominant and subordinate females for 'Other' (Chi-square test: χ^2=15.13, P<0.001, df=1). All individuals showed no interest in 'Enclosure vegetation'.

5.3.3 Feeding durations

A Kruskal-Wallis test indicated that there was a significant difference between individuals in the mean time spent feeding on fresh food and chow combined (H=14.88, P<0.01, df= 3). Differences in mean time spent feeding (fresh food and chow combined) occurred between the subordinate female and all the other individuals within the group (Two-sample sign tests: DM-SF Median=6.00, P<0.01; DF-SF Median=7.000, P<0.01; U-SF Median=-3.00, P<0.01). The dominant female spent a significantly longer mean time engaged in consumption of fresh food than the subordinate female (Figure 5.) (Two-sample sign test: Median=7.00, P<0.01).

5.3.4 Aggression

The mean number of aggressive interactions initiated during non-feeding and feeding observations for the spider monkey group can be observed in Figure 6.
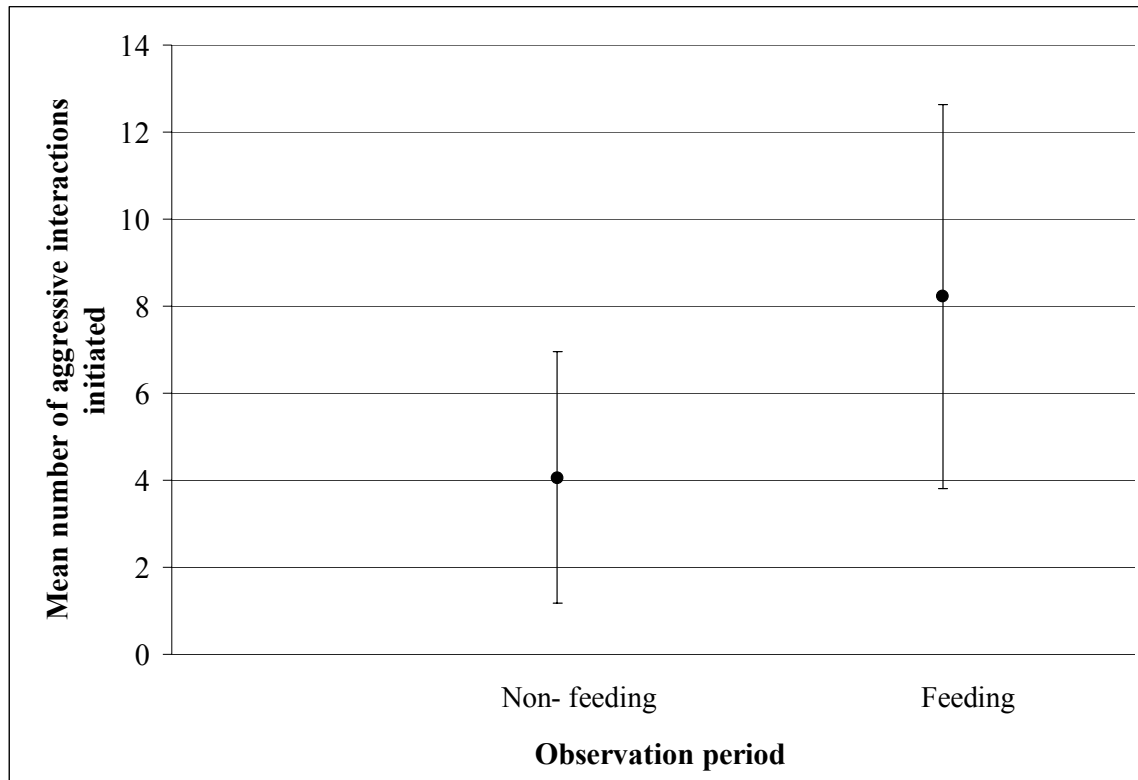

Figure 6. The mean number of aggressive interactions initiated during non-feeding and feeding observations for the spider monkey group. The error bars represent ± 1 S.D.

A two-sample t-test indicated that there was a significant difference in the mean number of aggressive interactions initiated during non-feeding and feeding observations (T=2.54, P<0.05, df=11).

The mean number of aggressive interactions initiated during feeding observations whilst the older individual (the subordinate female) of the spider monkey group was either present (i.e. with the remainder of the group) or absent (i.e. feeding separately) can be observed in Figure 7.
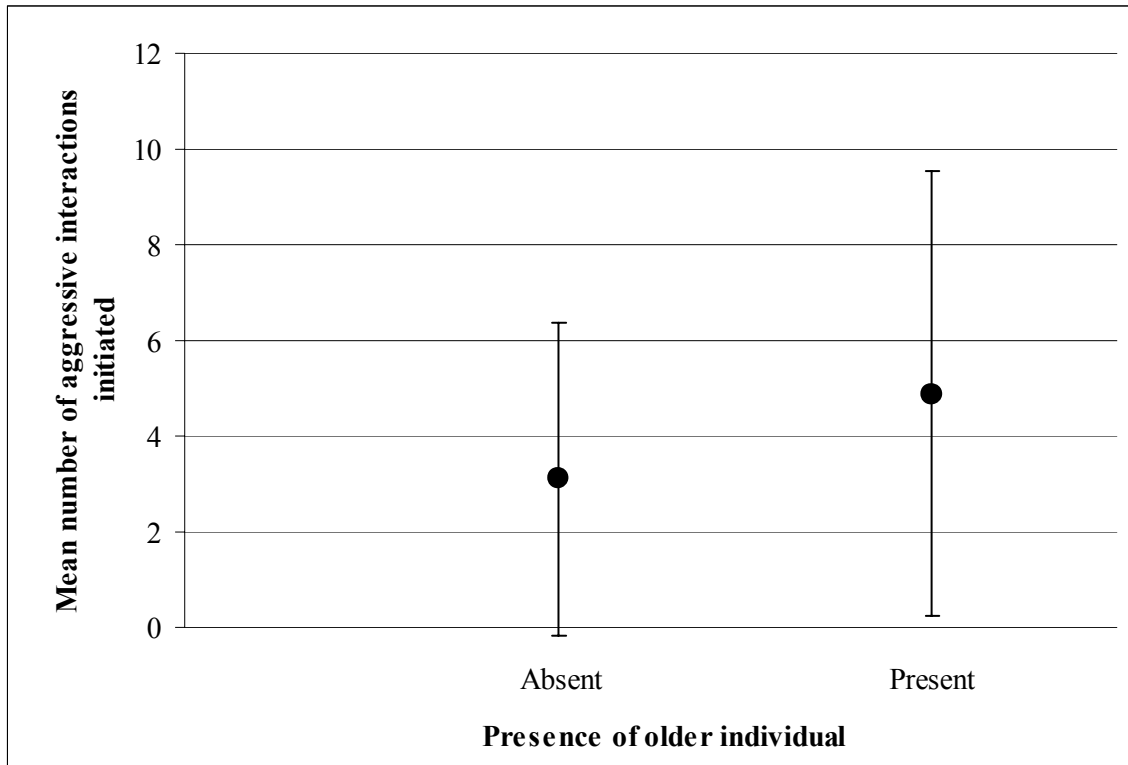
Figure 7. The mean number of aggressive interactions initiated during feeding observations whilst the subordinate female of the spider monkey group was present and absent from the remainder of the group. The error bars represent ± 1 S.D.

A two-sample t-test indicated that there was no significant difference in the mean log number of aggressive interactions initiated whilst the older individual was present and whilst absent (T=0.87, P=0.4, df=15).

5.4 Between-species comparisons

5.4.1 Food preferences

The mean time (minutes) spent feeding on fresh food (circles) and feeding on monkey chow (squares) for each species can be observed in Figure 8.
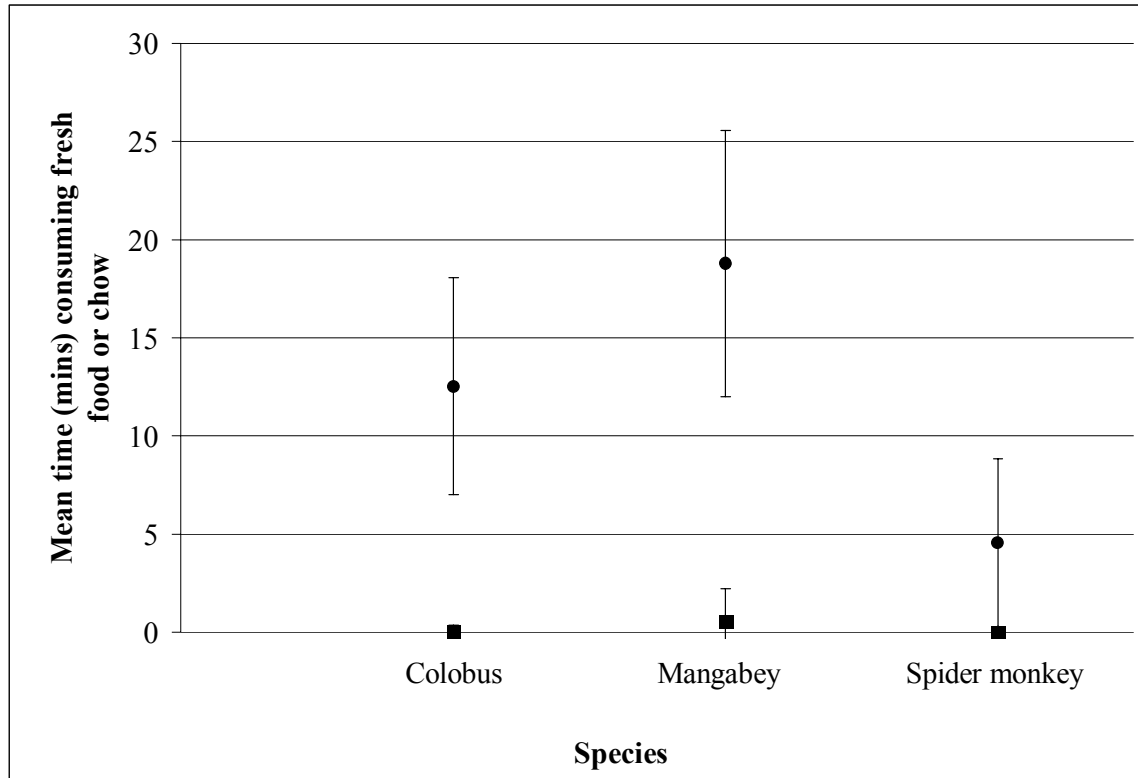
Figure 8. Mean time spent engaged in consumption of monkey chow (denoted by ■) and fresh food (denoted by ●) during observations of feeding periods for each species. The error bars represent ± 1 S.D.

The mean time spent feeding on monkey chow differed significantly between the species groups (Figure 8.) (Kruskal-Wallis test: H=8.00, P<0.05, df=2), with the mangabey group spending a significantly greater mean time feeding on monkey chow than the other groups (Mann-Whitney U-tests: Mangabey-Colobus W=1273.5, P<0.05; Mangabey-Spider monkey W=942.0, P<0.05).

The mean time spent feeding on fresh food differed significantly between the species groups (Figure 8.) (Kruskal-Wallis test: H=54.07, P=0.000, df=2), with the mangabey group spending a significantly greater mean time feeding on fresh food than the other groups (Mann-Whitney U-tests: Mangabey-Colobus W=1067.0, P<0.001; Mangabey-Spider monkey W=1309.5, P<0.001) and the colobus group spending a significantly greater time than the spider monkey group (Mann-Whitney U-test: W=2071.5, P<0.001).

5.4.2 Feeding durations

The mean time spent feeding on fresh food and chow combined differed significantly between the species groups (Kruskal-Wallis test: H=55.12, P=0.000, df=2), with the mangabey group spending a significantly greater mean time feeding (fresh food and chow combined) than the other groups (Mann-Whitney U-tests: Mangabey-Colobus W=1049.0, P<0.001; Mangabey-Spider monkey W=2068.5, P<0.001) and the colobus group spending a significantly greater time than the spider monkey group (Mann-Whitney U-test: W=1312.5, P<0.001).

5.4.3 Aggression

The mean number of aggressive interactions initiated by each species during non-feeding (baseline) observations can be observed in Figure 9.
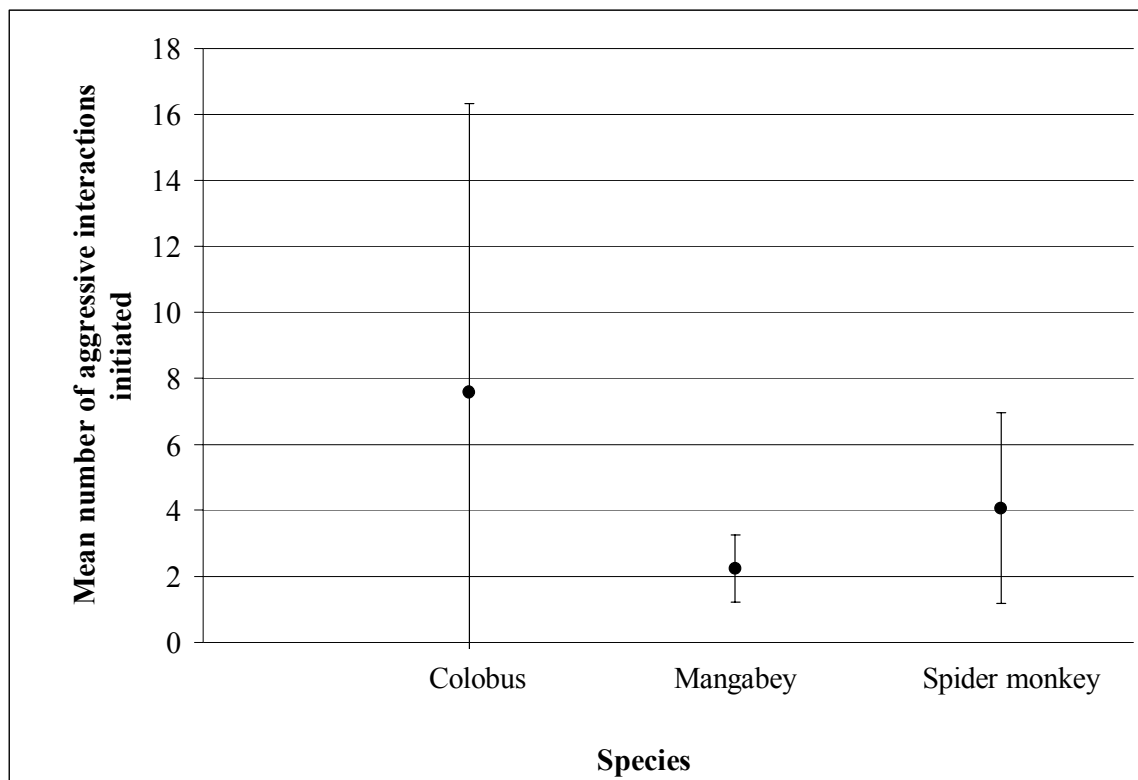

Figure 9. The mean number of aggressive interactions initiated during non- feeding observations for each species. The error bars represent ± 1 S.D.

The colobus group showed the greatest mean number of aggressive interactions initiated, followed by the spider monkey group, and then the mangabey group. The mean number of aggressive interactions initiated differed significantly between the species groups (Kruskal-Wallis test: H=6.53, P<0.05, df=2), with the colobus group exhibiting more aggressive interactions than the mangabey group (Mann-Whitney U-test: W=375.0, P<0.05), but with no differences between the other two species groups (Mann-Whitney U-tests: Colobus-Spider monkey W=378.0, P=0.2358; Mangabey-Spider monkey W=159.0, P=0.1092) (Figure 9.).

6. Discussion

6.1 Feeding behaviour within species

6.1.1 Food access

As approach to food and commencement of feeding was biased towards one individual in each of the species groups (Figures 1. and 3.), this suggests unequal resource access was occurring at the time the food was initially provisioned (Belzung & Anderson, 1986; Brennan & Anderson, 1988). Therefore, the hypothesis that access to food would not be equal between group members can be accepted at the time of food provisioning. This supports findings by Boccia *et al.* (1988) and Tovar *et al.* (2005), where the same few individuals always gained priority access to the food and commenced feeding first.

In this study, the first individuals to arrive and commence feeding were not the dominant males of the groups, disagreeing with predictions of male dominance-related food access in primate species (Furuichi, 1983; Emlen, 1997; Radespiel & Zimmermann, 2001). Within the mangabey group, the subordinate female most frequently arrived and commenced feeding first from the provisioned food during the study period. As mentioned, this does not support the predictions of male dominance (Radespiel & Zimmermann, 2001). Strong linear dominance hierarchies with males dominant over females are usually observed in mangabeys (Stahl & Kaumanns, 2003). However, the subordinate female of this group did have a young baby (aged ten days at commencement of the study), so it may be hypothesised that she was behaving

differently as would otherwise to gain access to food, or that she was allowed this preferential access due to the substantial increased nutritional and energetic requirements occurring during lactation (Warren & Crompton, 1998; Overdorff *et al.* 2005). It may be that priority food access for the mangabey group was altered slightly due to this influence of the newborn on the subordinate female. The next individual to most frequently access the food within this group was the dominant male, with the remaining individual of the group never achieving priority food access, therefore this may give support for this hypothesis. Further study outside of lactation would indicate whether this was the case.

There was also a significant difference in the number of scans the dominant male was engaged in feeding at the food, but only for the colobus group. Therefore, the hypothesis that the dominant male would remain in close proximity to the provisioned food whilst feeding can be accepted only for this group. Previous research has shown that dominant individuals will feed nearer to the provisioned food than subordinates (Deutsch & Lee, 1991; Blois- Heulin & Martinez- Cruz, 2005). Within the mangabey group, in addition to the dominant male, the subordinate female was also observed engaged in feeding at the food for a greater number of scans in comparison to the remaining individual of the group (Table 6.). As already discussed, she did have the young baby, and again, it could be hypothesised that her behaviour differed and she was either obtaining or permitted this access due to lactational energetic requirements (Warren & Crompton, 1998; Overdorff *et al.* 2005).

The dominant female of the mangabey group was observed to feed preferentially greater than two metres from the provisioned food. Outside of formal observations, it was noted that during feeding observations this individual would often snatch and hoard several food items from where provisioned and carry these away to feed at distance greater than two metres from the food. This practice has also been observed in rhesus monkeys (Deutsch & Lee, 1991; Brennan & Anderson, 1998). Food snatching seems to occur more frequently in subordinate individuals (Brennan & Anderson, 1998). This behavioural strategy is thought to be employed by subordinate individuals to ensure adequate food intake is maintained, whilst avoiding competition or aggression from dominant individuals at the food site (Deutsch & Lee, 1991). This particular individual observed snatching the food was the dominant female of the group. As mentioned previously, dominance hierarchies in captive mangabeys are strongly linear with males dominant over females (Stahl & Kaumanns, 2003). The dominant female may

have been trying to avoid conflict at the food site from the dominant male. The subordinate female however, did not demonstrate this food snatching behaviour, but again, behaviour may have differed due to the influence of the newborn.

Examining feeding durations, no significant differences were observed in time spent engaged in food consumption between individuals of the mangabey group. Therefore, although proximity to the provisioned food whilst feeding did differ significantly for the dominant female, as overall feeding duration did not, it could be hypothesised that she was employing this food snatching strategy to maintain intake whilst minimising conflict at the food site (Deutsch & Lee, 1991). Further study outside of lactation would indicate whether this was the case.

6.1.2 Food preferences

Overall, monkey chow can be considered unappealing to these primate groups (Figures 2., 4. and 5.). Across all species, chow consumption was only recorded on nineteen occasions for four individuals (including males/females, dominants/subordinates), though with at least one representative from each species group. Consumption of chow, both in itself and in comparison to fresh food was low. The hypothesis that fresh food would be preferred over monkey chow can be accepted. Previously, Addessi *et al.* (2005) demonstrated that tufted capuchin monkeys showed a preference for fresh foods in comparison to monkey chow. It has also been shown that captive primates will not necessarily consume an equal balance of all the food types provided, but feed preferentially on more appealing foods (Oftedal & Allen, 1996).

Only the subordinate female (the elderly individual) from the spider monkey group demonstrated no significant difference in chow and fresh food consumption. However, this individual was only observed feeding in seven scans. Therefore, the likelihood of obtaining a significant result was small. Examination of the food types consumed within these scans reveal chow was never selected (Figure 5.). Although a significant result was not obtained, a preference for fresh food over chow can still be demonstrated.

Monkey chow is provisioned with the intent of meeting, as far as possible, the necessary energetic and nutritional requirements of primates (BANR, 2003; Addessi *et al.* 2005). For this reason, it may be expected that as chow consumption is low, the welfare of

individuals is below optimum. The sole consumption of fresh food may not be adequate for captive primate groups as, being cultivated, fresh foods do not duplicate the nutritional content of foods eaten in the wild by free-ranging individuals (Nijboer & Dierenfeld, 1996). Consumption of monkey chow was noted to occur on occasions during non-feeding observation periods (utilising focal sampling). However, time constraints restricted analysis of such data. Therefore, total chow consumption for these species groups cannot be ascertained. It is possible that chow may be selected by individuals more as time progresses once the majority of the fresh food is consumed. Feeding observation periods may reflect only the immediate preference for chow in comparison to fresh foods. To determine whether this is the case, additional analysis of data collected during non-feeding periods is suggested as an area of future study. This should identify the true, not simply the immediate appeal of monkey chow to these species groups, and can allow determination of whether adequate chow consumption is a necessity for optimal captive primate welfare.

For each species group, all individuals indicated preferences within the fresh foods provisioned (Tables 4., 7. and 9.). Crissey (2005) previously commented that individual preferences may impact upon the balance of foods consumed by primate groups. Within the species groups, dominant and subordinate individuals often illustrated preferences for the same fresh food types. Therefore, the hypothesis that the dominant male will consume his preferred food type(s) thus leaving less choice for subordinate group members can be rejected. Barton & Whiten (1993) observed no significant difference in type of foods consumed with regards to dominance rank for free-ranging olive baboons. Addessi *et al.* (2005) and Laska *et al.* (2000) also showed a lack of significant variation in patterns of food preference in captive tufted capuchin monkeys and spider monkeys, respectively, supporting this study.

The fresh food type 'Other' was preferred by individuals from all species groups, with one exception (the unknown juvenile individual from the spider monkey group). Such common preferences across varying species, ages and dominance ranks therefore indicate this food type is potentially highly desirable to all individuals. Raisins, monkey nuts, and seed/ nut mix were included under this food type categorisation (see Appendix 1 for complete definition). Within dominance-dyads, significant differences in the number of scans feeding were only observed for 'Other'. These occurred for the mangabey and spider

monkey groups between the dominant and subordinate females (Tables 7. and 9.). As this was the only preferred food type that elicited dominance-related differences, and highlights the potential occurrence of competition between dominant and subordinate group members (Barton & Whiten, 1993), this again gives support that the food type 'Other' is highly desirable. However, despite priority access for dominant individuals occurring on occasion for 'Other', access appears not to be restricted to such a degree, as consumption of this particular food was recorded frequently enough for it to be deemed a preferred type for all individuals, excepting one. Therefore, significantly biased food access seems an unlikely issue for the groups involved in this study (Crissey, 2005). Furthermore, slight preferential access is expected and is normal practice for dominant individuals in primate groups (Furuichi, 1983; Emlen, 1997), provided this does not go so far as to impact upon welfare (Crissey, 2005).

6.1.3 Feeding durations

It has been previously observed in some captive primates that time spent feeding is not equal between group members (Belzung & Anderson, 1986; Brennan & Anderson, 1988). Greater feeding durations have been observed to occur for the dominant individuals (Janson, 1985; Belzung & Anderson, 1986; Brennan & Anderson, 1988; Saito, 1996). In this study, no significant differences in feeding durations between individuals were observed for fresh food and chow combined, except for the subordinate female from the spider monkey group (discussed later). Therefore, the hypothesis that food consumption would not be equal between group members can be rejected. There is no significant difference in the time spent feeding by dominant and subordinates individuals, therefore the hypothesis that the dominant male would feed for longer can be rejected. Post *et al.* (1980) also did not observe any variation in time spent feeding with regards to dominance rank in free-ranging yellow baboons *Papio cynocephalus*.

As time feeding did not differ significantly in this study, access to food and in turn, food intake between individuals is expected to be more equal. Disproportionate energetic gains and any welfare implications potentially resulting from these (Crissey, 2005), which have been observed in previous work (See Janson, 1985; Barton & Whiten, 1993; Saito, 1996) should therefore be unlikely to occur for the groups involved in this study. Results obtained are therefore similar to that of Deutsch & Lee (1991), where no differences in food intake were

observed between rhesus monkeys of different rank. Regarding the implications for feeding strategies, this is indicative that the procedure of food provisioning utilised at ZSL London Zoo is effective, dispersed widely enough to allow for equal resource access for all individuals (Michels, 1998; Blois- Heulin & Martinez- Cruz, 2005; Crissey, 2005). The information obtained from these findings can be used to help with the development of provisioning practices for captive primate populations (Nijboer & Dierenfeld, 1996; BANR, 2003). For the species groups in this study, food was provisioned in wide clumps, with several food clumps distributed across the enclosure. Application of such a provisioning strategy for primates in other institutions should therefore contribute towards effective captive primate feeding.

As stated earlier, a significantly lower feeding duration was observed for the subordinate female from the spider monkey group. As this individual is considerably older, it is possible that appetite may be reduced due to age (Ingram *et al.* 2005). However, it is important to consider this significant result, as lower feeding durations potentially indicate insufficient food access and energetic intake (Whitten, 1983; Crissey, 2005). Principally, separation during feeding takes place to ensure this does not occur (T. Lee, pers. comm.). However, this individual receives additional food, consisting of rice, oats and crushed chow, which is hand-fed. This supplementary provisioning may increase overall calorific intake (Lintzenich & Ward, 2001), though it was not included in feeding durations as it was not possible for the observer to move between the indoor and outdoor viewing areas during an observational period.

With further reference to this latter point, feeding events may have been occurring at any time during feeding observations that could not be recorded and included within analyses. Therefore, the true feeding duration for this individual may not necessarily be as low as assumed from the results, and the figure obtained may not be fully representative. Significance of feeding duration in comparison to other group members may not be reliable for this individual. Therefore, care should be taken with interpretation of results. However, on-going monitoring of this particular individual by keeping and veterinary staff is highly recommended.

6.1.4 Feeding and aggression

Numerous studies have noted that aggressive interactions occur more frequently when groups of both free-ranging and captive primates are feeding as opposed to when undertaking other activities (See Wasserman & Cruickshank, 1983; Janson, 1985; Saito, 1996; Sterck & Steenbeek, 1997; Pruetz & Isbell, 2000). In patas monkeys *Erythrocebus patas*, rates of aggression during feeding were nearly greater 50% than when not feeding (Pruetz & Isbell, 2000). Results obtained for the spider monkey group were similar to previous findings, with a significantly higher number of aggressive interactions initiated during feeding as opposed to non-feeding periods.

Aggression during feeding observation periods was only carried out for the spider monkey group as the opportunity arose, which was not available for the other two species, to collect this additional data. With regards to potential further research however, investigation of aggressive interactions between feeding and non-feeding observation periods additionally for the colobus and mangabey groups could allow for determination of a similar relationship occurring as observed for the spider monkey group, and for comparisons between the species.

It is likely that within the spider monkey group that there is aggression occurring over food (Figure 6.). However, as no significant differences were observed in feeding durations, apart from for the subordinate female, implications potentially resulting should therefore be unlikely to occur for the individuals of this group (Crissey, 2005). While aggression is understandably expected to occur more frequently during feeding (Wasserman & Cruickshank, 1983; Janson, 1985; Saito, 1996; Sterck & Steenbeek, 1997; Pruetz & Isbell, 2000), as this does not appear to impact upon welfare, the feeding practice is considered appropriate.

A potential issue is highlighted, however, regarding the subordinate female from the spider monkey group. As a significantly lower feeding duration was observed for this individual, yet no other, it may be hypothesised that the elevated levels of aggression during feeding periods are affecting the subordinate female and causing this observed result. Previously, it has been shown that subordinate individuals experience aggression more whilst feeding (Deutsch & Lee, 1991), and often individuals who frequently experience aggression whilst feeding exhibit the lowest feeding durations (Post *et al.* 1980). Further examination of aggressive interactions indicates, however, that there was no significant

change in the behaviour of the other spider monkeys when the subordinate female re-joined the group (Figure 7.). The increase in aggression during feeding observation periods does not appear to be aimed specifically at the subordinate female. Again as mentioned earlier, although the feeding durations of the subordinate female are significantly lower, feeding by this individual was frequently carried out indoors. As it was not possible for the observer to move between the indoor and outdoor viewing areas during an observational period, feeding events may have been occurring that could not be recorded and included within analyses, therefore the true feeding duration for this individual may not necessarily be as low as interpreted from the results.

The benefit of the brief period of separation of the elderly subordinate female from the remainder of the spider monkey group to allow for feeding cannot be fully determined at this stage. Obtaining a significantly lower feeding duration could indicate that this individual is not obtaining sufficient energetic intake (Whitten, 1983; Crissey, 2005). However, without allowing for inclusion of the supplementary food provisioned specifically for this individual, or the feeding events which could not be recorded, a definite welfare detriment cannot be confirmed. On the other hand, separation, with regards to the behaviour of the remainder of the group towards this individual, is not detrimental (Figure 7.). At present, there is no indication that the period of separation for feeding should be halted. However, on-going monitoring of the situation, and the elderly subordinate individual, should take place, with potential further study.

6.2 Between species

Variation between species groups was observed with regards to feeding behaviour (Figure 8.) and within-group aggression (Figure 9.).

Interestingly, the mangabey group demonstrated the highest feeding duration, and also the lowest aggression rate. Feeding durations were seen to increase when rates of aggression in free-ranging yellow baboons were lower (Post *et al.* 1980). It is possible that within the mangabey group that as aggression, and therefore competition for food occurred significantly less, there was more time available for feeding.

Conversely, the colobus group demonstrated a significantly lower feeding duration than the mangabey group, yet a significantly greater rate of within-group aggression.

Therefore again conversely, it is possible that feeding durations were lower due to the increased occurrence of aggression. Captive mangabeys usually show linear, male-dominant hierarchies (Stahl & Kaumanns, 2003). In captivity however, black and white colobus monkeys have been shown not to demonstrate clear dominance hierarchies (Björnsdotter et al. 2000; Pruetz & Isbell, 2000; Gron, 2007b). It could be hypothesised therefore that in the mangabey group, as ranking is determined and known by the individuals within the group, competition for food occurs less, with more time available for food consumption (Deutsch & Lee, 1991; As observed by Post et al. 1980), whereas for the colobus group, with no defined ranks (Björnsdotter et al. 2000; Pruetz & Isbell, 2000; Gron, 2007b), food competition may occur more frequently and therefore less time is available for food consumption (Deutsch & Lee, 1991). As rates of aggressive interactions were calculated from non-feeding observations however, determination of aggression during feeding periods would instead be required to confirm this. Despite aggression being significantly greater for the colobus group, no significant differences were observed in feeding durations between the individuals of this group, and therefore detrimental impacts and any welfare implications potentially resulting from this greater aggression rate are not anticipated (Crissey, 2005).

Feeding durations were observed to be significantly lower for the spider monkey group compared to both the mangabey and the colobus groups (Figure 8.). It is possible that this group does exhibit lower feeding durations, especially as this group included the elderly female. However, this assumption cannot be confirmed due to differing methods, with data of a slightly different nature having to be collected for the spider monkey group. This difference was required due to the fact that it was not possible for the observer to move between the indoor and outdoor viewing areas during an observational period. However, group members may have been feeding indoors additionally, where such behaviour could not be recorded and included within analyses, meaning the true group feeding duration may not necessarily be as low as interpreted from the results. Significance of comparisons between species may not be consistent, and caution should be taken regarding interpretation and application therefore. However, inclusion of the spider monkey group within this study would not have been possible if it were not for these differing methods of data collection, and there were specific requests to study this particular species group (A. Hartley, T. Lee, pers. comm.).

6.3 Implications of study findings

This study highlighted, as has been shown previously (See Crissey, 2005), that developing appropriate diets for captive primates is a complex process. However, the potential application of findings obtained is indicative of the use of behavioural and zoo studies towards improving the management of captive species.

Unequal resource partitioning was not observed, as demonstrated by non-significantly differing individual feeding durations, and provisioned food was dispersed widely enough as to negate the occurrence of monopolisation. The study is indicative that the feeding strategies utilised at ZSL London Zoo for these three captive primate species are effective. Application of these strategies would therefore benefit captive primate feeding in other institutions, allowing further insight to be gained into the factors influencing feeding (Laska *et al.* 2000), and contributing to the on-going development of 'scientifically sound' diets and feeding provisioning strategies (Nijboer & Dierenfeld, 1996; BANR, 2003; Addessi *et al.* 2005; BIAZA, 2005).

The critically endangered white-naped mangebey (IUCN, 2007) is currently only represented by ~fifty individuals in breeding centres worldwide (WAPCA, 2008; Wolters, 2008). Improvement of feeding practices to allow for better captive care of this species could increase this figure, having major implications for its conservation (Wielebnowski, 1998; BIAZA, 2005; Wharton, 2007).

Additionally, potential application of findings as models to other primate species can allow for improvement of feeding practices, and therefore extend the variety of conservation-concern species in captive breeding programmes without repetition of research. Endangered species of both colobus and spider monkeys exist (Eastern red colobus *Procolobus rufomitratus*: Critically Endangered, White-whiskered spider monkey *Ateles marginatus*: Endangered, Variegated spider monkey *Ateles hybridus*: Critically Endangered) (IUCN, 2007). Further research is required to determine and ensure the use of the species from this study as models are appropriate, yet this may potentially provide a key benefit for primate species of conservation concern.

Conclusions

There is a need to address feeding practices to successfully manage and propagate primates of conservation concern (Boccia *et al.* 1988). Improvement of feeding success can help to negate existing problems with diet composition and provisioning strategies that are still present for many captive-held species (Schwitzer & Kaumanns, 2003). Optimisation of captive primate health, well-being and welfare should then result (Zinner, 1999; Addessi *et al.* 2005; Tovar *et al.* 2005), contributing to the improvement of breeding programmes (Edwards, 1997; Wielebnowski, 1998; Zinner, 1999).

The importance of the role of captive breeding for conservation has been emphasised for some time (Wielebnowski, 1998; BIAZA, 2005), and improvement of the current varying success rates of breeding programmes would be beneficial (Edwards, 1997; Wielebnowski, 1998). This has important and obvious advantages for primate species of conservation concern (Edwards, 1997; Wielebnowski, 1998; Zinner, 1999; Wharton, 2007).

7. Acknowledgements

Word count: 10,285 (excluding Acknowledgements, References and Appendices).

8. References

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9. Appendices

9.1 Appendix 1: Definition of food types

Food type	Definition of what constitutes food type
Monkey chow	Pellet food: Leaf Eater, Old World Monkey or Trio rings, as appropriate for species.
Fruit	Apple, banana, grapes, orange, pear, soft fruit.
Vegetable	Avocado, beetroot, corn on cob, cucumber, fennel, leek, parsnip, pepper, potato, root vegetable mix (Parsnip, potato, sweet potato), sweet potato.
Greens/browse	Chicory, iceberg lettuce, leafy greens, (kale, spinach and frisseé).
Enclosure vegetation	Any vegetation type growing within the enclosure, not specifically provisioned at feeding times. Includes common grasses and weed plants.
Other	Eggs, live food (locusts, crickets, mealworms), raisins, seed/nut mix, monkey nuts.

9.2 Appendix 2: Detailed feeding schedules

Black and white colobus *Colobus guereza kikuyuensis*

Morning provision	Afternoon provision
• 400g Leaf Eater/ Old World Monkey pellets • 500g Leek/fennel • 600g Leafy greens • 500g Parsnip, potato, sweet potato	• 200g Leaf Eater/ Old World Monkey pellets • 300g Leek/fennel • 600g Leafy greens • 500g Parsnip, potato, sweet potato • 800g Corn on cob • (Pinch of vionate)

White- naped mangabey *Cercocebus atys lunulatus*

Morning provision	Afternoon provision
• 100g Leaf Eater/ Old World Monkey pellets • 450g Leafy greens • 350g Apple • 25 Grapes • 2 Corn on cob	• 80g Leaf Eater/ Old World Monkey pellets • 300g Leek/fennel/pepper • 650g Leafy greens • 300g Banana • 300g Pear • 290g Soft fruit • 200g Orange • 350g Root vegetable mix • 3 Eggs (only 3 days per week) • (Pinch of vionate and ½ scoop Calcium lactate)

Red- faced black spider monkey *Ateles paniscus*

Morning provision	Afternoon provision
• 200g Trio rings/Old World Monkey pellets • 2 Apples • 30 Grapes • 2½ Bananas (hand fed) • 2 Pears • 400g Soft fruit • 300g Beetroot/parsnip/sweet potato • 200g Corn/cucumber/fennel • 400g Chicory/friseé/spinach • 45g Live food • 1 egg (only 3 days per week) • For elderly individual only- Baby rice and oats with crushed pellet, ½ avocado (hand fed) • (1 scoop protexin)	• 150g Trio rings/Old World Monkey pellets • 2 Apples • 40 Grapes • 2 Pears • 600g Soft fruit • 400g Beetroot/parsnip/sweet potato • 250g Corn/cucumber/fennel • 500g Chicory/friseé/iceberg lettuce/ spinach • 1 Avocado • (Pinch of vionate)

9.3 Appendix 3: An ethogram of state behaviours recorded using instantaneous sampling in all groups

Behaviour	Definition
Feeding	Actively consuming food, through either reaching for, holding/ handling food, placing food in the mouth or chewing (Adapted from Range & Noë, 2002).
Foraging	Searching for food through manipulating environment/ substrate, including

	enrichment devices, with attention directed towards potential foods. Individual may be stationary or moving slowly.
Drinking	Actively drinking at provisioned water source, either bottle or other.
Social *(see below)*	• 'Aggression' • Affiliation • Grooming • Sexual behaviour • Play
Locomotion	Moving, either walking, climbing or running, where the distance covered exceeds one body length (Bernstein & Baker, 1988).
Resting/ sleeping	Not partaking in any other behaviour/ activity or interacting socially, eyes may be closed though not necessarily asleep (Bernstein & Baker, 1988); sleeping.
Out of sight	Not visible, either due to be being hidden within enclosure e.g. behind substrate/ within vegetation, or present in another section of enclosure not visually accessible.

Social behaviours- further definition

Social behaviour	Definition
'Aggression'	Includes aggressive contact, threat or displacement *(see below)*.
Affiliation	Includes huddling together of individuals with extensive body contact for an

	extended period of time, or mutual embrace with individual contact less extensive and for a shorter period of time.
Grooming	• *Auto- grooming:* Repetitively searching through and manipulating own fur with hands/ mouth (Nickelson & Lockard, 1978). • *Allo- grooming:* Repetitively searching through and manipulating fur of another individual with hands/ mouth (Adapted from Wojciechowski, 2004).
Sexual behaviour	Includes sexual presentation of female genital area towards male, mounting of female by male, or copulation- intromission of penis, thrusts repeatedly, may/ may not ejaculate (Nickelson & Lockard, 1978; Reed *et al*, 1997).
Play	Either solitary or alongside others, includes interaction with environment/ other individuals, often in an active, lively manner (Adapted from Anaya- Huertas & Mondragón- Ceballos, 1998).

'Aggression' behaviours- further definition

'Aggression' behaviour	**Definition**
Aggressive contact	Biting, pulling or grabbing another individual, with intent to cause harm.
Threat	Stare directed at target individual from aggressor (Range & Noë, 2002). Aggressor

	may make a sudden, aggressive lunge/ movement towards the target individual, with or without chase (Nickelson & Lockard, 1978).
Displacement	Supplanting of target individual by 'aggressor', either by presence, stare, or by physical means (Adapted from Nickelson & Lockard, 1978).

Aggressive event behaviours- further definition

Aggression event behaviours	**Definition**
Biting	Aggressor makes contact with pressure from mouth and/or teeth on any area of body of target individual, with active intent to cause harm.
Pulling	Aggressor makes contact with hands/feet on any area of body of target individual and applies force while maintaining grip.
Grabbing	Aggressor makes forceful contact with hands/feet on any area of body of target individual.
Lunge	Sudden, aggressive movement towards target individual, not followed by a chase (Range & Noë, 2002).
Chase	Aggressor charges at target individual and pursues as the target individual flees (Reed et al, 1997).