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Feeding strategies in sympatric red howler monkeys (*Alouatta seniculus*), saddleback tamarins (*Saguinus fuscicollis*) and squirrel monkeys (*Saimiri boliviensis*), in the Pacaya-Samiria national reserve, Peru

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Abstract

This study investigated the feeding strategies of sympatric red howlers (*Alouatta seniculus*), saddleback tamarins (*Saguinus fuscicollis*) and squirrel monkeys (*Saimiri boliviensis*) in the Pacaya-Samiria National Reserve, Peru. The habitat types occupied during all behaviours and purely when feeding differed significantly between the three species ($p < 0.005$). The overall diet consumption was also shown to be significantly different between the three species ($p < 0.005$). These results demonstrated that niche separation between these sympatric primates may be achieved through differences in habitat types used for foraging and food types consumed. Data from this study was compared with data collected at the same site using the same methods in 2011. The diet composition differed significantly within each of the species between 2011 and 2012 ($p < 0.005$). It could be proposed that factors such as changes in climate may have an impact on the rainforest ecosystem, and consequently affect the feeding strategies of primates, however further research is required to determine if this is the case and the exact impacts this would have on the primates.

Key words: Neotropical primates, diet, habitat, niche separation

Introduction

The diet and feeding strategies of primates provide improved knowledge as to how different species function and interact in their ecological communities (Pickett *et al.*, 2012). Furthermore, feeding behaviour is strongly linked to the vegetation structure and availability of food sources (Simmen and Sabatier, 1996). There is rising concern that both human interference and global environmental change are causing adverse impacts upon the rainforest (Mittermeier and Konstant, 2001). It is therefore important to gain a greater understanding of primate feeding strategies, so that this knowledge can be used to help preserve the natural environment of rainforest primates.

The Pacaya-Samiria National Reserve is the largest protected area of rainforest in Peru. The native human populations of this area have been gradually growing, increasing the need for agriculture, hunting and use of the forest resources, potentially impacting the rainforest ecosystem (Kvist and Nebel, 2001). Furthermore, the habitat type utilised by primates is influenced by the food resources available to them, and is further determined by the seasonality of food production that occurs in tropical forests (Porter *et al.*, 2007; Stone, 2007). Global environmental change has been suggested to affect the dynamics of the dry and wet seasons, with differences in the amount of flooding in addition to the time periods in which this occurs (Malhi *et al.*, 2008). As this is likely to affect the reproduction of the plants, this may have adverse impacts on the food availability to the primates and ultimately have devastating effects on the rainforest ecosystem (Grogan and Schulze, 2011).

Various species of primates are found in the Pacaya-Samiria National Reserve. Red howlers (*Alouatta seniculus*) are primarily diurnal folivores, consuming leaves (Wallace *et al.*, 2008), but both squirrel monkeys (*Saimiri boliviensis*) and saddleback tamarins (*Saguinus fuscicollis*) are diurnal frugivore-insectivores, consuming fruits and insects (Boinski, 1999; Rylands *et al.*, 2008). However there are examples of niche separation suggested to reduce the interspecific competition between these species. Squirrel monkeys are found in large group sizes, usually ranging between 25-75 individuals (Boinski, 1999) and spend 75-80% of their day foraging for insects and animal prey (Lima and Ferrari, 2003). Although they use all levels of the forest, squirrel monkeys forage and travel predominantly in the lower canopy and understory (Boubli *et al.*, 2008). Saddleback tamarins are found in smaller groups of 2-15 individuals, with diets consisting mainly of arthropods, but have also been found to include vertebrates such as frogs and lizards (Smith, 2000). Most time is spent occupying the lower canopy and understory, up to 10m above ground (Rylands *et al.*, 2008). Red howlers are found in even smaller groups, averaging between 4-10 individuals. Their folivorous diet means they have very different activity budgets, spending up to 70% of the day resting in the upper canopy (Wallace *et al.*, 2008). Of the Neotropical primates they are the most widely distributed and have the largest range of habitats (Agostini *et al.*, 2010). However, all three species have been shown to vary in foraging behaviour, such as day range and diet composition, depending on the seasonality of food distribution and availability (Smith, 2000; Stevenson *et al.*, 2000; Stone, 2007).

There are a range of factors that influence primate feeding strategies. Mixed-species troops are sometimes formed, in which co-operation increases foraging efficiency (Porter and Garber, 2007). Squirrel monkeys often form interspecific interactions with

capuchins. As these live higher up in the canopy, squirrel monkeys take advantage of their fallen opened fruit, which would normally be unavailable, and the disturbance they cause, which exposes insects (Pinheiro *et al.*, 2011). Saddleback tamarins are often found living sympatrically with other tamarin species in mixed groups, which gives advantages of greater predator detection and more efficient resource utilization via a greater amount of prey captured and improved defence of resources (Smith, 2000). However previous studies have shown that sympatric species that live in the same trophic level should display variation in their ecological niches in order to reduce interspecific competition (Nadjafzadeh and Heymann, 2008).

This study aimed to compare the feeding strategies of sympatric saddleback tamarins, squirrel monkeys and red howlers in the Pacaya-Samiria National Reserve in Peru, to investigate whether there are differences as a result of niche separation to reduce intraspecific competition between the three species. It was hypothesised that this could be achieved by using different habitat types or consuming different food types. Therefore the habitat type was recorded across all behaviours observed, then analysed to see if each species utilised a specific habitat when feeding. Furthermore, data was collected on food preference and examined to determine if each species displayed any differences in diet composition.

Methods

Study Site

The study was conducted in the Pacaya-Samiria National Reserve in Peru (Fig. 1). The reserve is 200,000km² and bordered by the rivers Ucayali and Marañón. The majority of land comprises of low-lying flooded forest, in addition to upland forest and palm swamp. Based at the PV2 Tascha watchpoint, six surrounding transects were used for data collection (Table I). Each transect was 2km long and randomly located following Peres (1999) (Fig. 2.). The transects included a range of forest types (terra firma, varzea and aguajale). Specific habitats were classified within each of these depending on the vegetation type (Table II). The climatic oscillation of the rainforest gives rise to distinct seasons. The wet seasons occurs between October and April and the dry season between May and September.



Figure 1: Location of the Pacaya-Samiria National Reserve, Peru



Figure 2: Location of the six transects where data collection was conducted in the Pacaya-Samiria National Reserve, Peru

Table 1: GPS Coordinates recorded at the end of transects used for data collection in the Pacaya-Samiria National Reserve, Peru

Location	GPS Coordinates
PV2 Tascha watchpoint	4°52'45.74" S 74°21'24.44" W
Transect 1	4°53'37.84" S 74°21'06.00" W
Transect 2	4°51'44.14" S 74°22'28.87" W
Transect 3	4°52'19.27" S 74°20'45.89" W
Transect 4	4°53'09.71" S 74°22'14.03" W
Transect 5	4°54'14.28" S 74°21'50.28" W
Transect 6	4°51'34.54" S 74°22'58.12" W

Table 2: Descriptions of specific sub-categories of habitats in which primates were observed in the Pacaya-Samiria National Reserve, Peru

Habitat Type	Description
Riverine	Forest located immediately next to the river with a sloping canopy. Dense vegetation changes throughout the year relative to the flood line, through ecological succession.
Liana	Low to intermediate canopy height. Dry, sandy soils. Densely populated with liana vines. No hardwood trees.
Open Understory	Sparse sunlight penetration, meaning there are large trees and a dense, high canopy cover but little ground flora. Higher concentrations of tannins within the leaves gives a darker colour to the vegetation, particularly fallen leaves.
Levee	Seasonally flooded, but have a greater percentage of ground flora than other habitats due to higher ground levels (this gives a characteristically lower flood line.) Dense understory vegetation. Can be divided further into two subcategories of Restinga and Restinga Bajjal.
Tree Fall Gap	Areas of the forest where trees have fallen, creating a unique habitat in which the canopy has been broken and sunlight can penetrate, resulting in a high percentage of ground flora.
Palm Swamp	Permanently flooded forest, due to bad drainage of soil, with a high prevalence of palms. Can be divided into pure swamps (only palm species) or mixed swamps (palm and other tree species.)

Study Group and Data Collection

Different troops, contrasting in size and composition, of squirrel monkeys, saddleback tamarins and red howler monkeys were observed within the reserve. Different groups could not be distinguished and none of the monkeys were fully habituated to human presence. The number of observations and observation times of each species varied every day, depending on whether a group could be located. Also, the group was sometimes lost either due to moving out of site or due to weather permitting conditions such as rain. Data collection occurred from 20th June 2012 until 6th August 2012. Transects were conducted daily between 7:00 to 13:00 and 14:00 to 17:00. As soon as the target species was found, the same group were followed for as long as possible for the extent of the data collection period. For each group located, the number of individuals and age-sex classification were noted using the following criteria: Infants (<18 months), juvenile (18-48 months), adult female (>48 months) and adult male (>60 months). At three minute intervals instantaneous scan samples (Altman, 1974) were undertaken, recording each individual's behaviour (locomotion, resting, feeding, social and vigilance; Table III). When

feeding, the type of food was recorded (insects, fruit, flowers, leaves, gums and seeds) noting the species of plant or animal where possible. The weather conditions, forest type and habitat type were recorded with every scan. Also, it was noted if any other species of primate were present, specifying the number of individuals and age-sex composition where possible. Height of the highest and lowest monkey of the group was estimated with each scan. Data was also available from 2011, which was collected by Operation Wallacea using the same methods as stated above, except five minute intervals were used opposed to three minutes.

Table 3: Ethogram of behavioural categories applied to data collection of sympatric saddleback tamarins, squirrel monkeys and red howlers in the Pacaya-Samiria National Reserve, Peru

Behaviour	Description
Locomotion	Movement, including walking, running and jumping between or within trees
Resting	Monkey inactive whilst standing, sitting or lying
Feeding	Visible foraging for food, manipulation of food or consuming food
Social	Interaction with one or more members of the troop, including grooming, playing, communication and fighting
Vigilance	Monkey standing in an upright position, looking alert and scanning the surrounding area
Other	Behaviour differing to those stated above
Out of sight	Monkey not visible during observation

Data Analysis

The data from all scan samples were separated into categorical data. Therefore differences in the proportions of different habitats used by different species were analysed by chi-squared. This was also conducted for the different habitats used when only feeding was observed, and for the different food types consumed by different species. The data provided from 2011, which was also separated into categorical data, was compared with data from 2012. Chi-squared was again used to analyse the proportions of different food types consumed by each species across the two years.

Results

Importance of Habitat in Feeding Strategies

To establish whether there were any differences between the habitats occupied by saddleback tamarins, squirrel monkeys and red howlers, the percentage of habitats utilised by each species when displaying all behaviours was first analysed (Fig. 3.) The number of observations were most frequent for squirrel monkeys (n=2931), however were similar for saddleback tamarins (n=1226) and red howlers (n=1098). Overall there was a significant difference between the habitats occupied by the three different species ($\chi^2=1355.283$, d.f.=10, $p<0.005$). All three species demonstrated a similar occupation of levees (saddleback tamarins 68.27%, squirrel monkeys 60.80% and red howlers 67.36%). The only other major habitat utilised by red howlers was palm swamps (22.10%), which were rarely used by saddleback tamarins or squirrel monkeys (1.39% and 3.34% respectively). Saddleback tamarins spent a notable proportion of time occupying lianas (22.59%) as did squirrel monkeys, but to a lesser extent (11.05%). Squirrel monkeys also occupied open understory and riverine habitats at similar frequencies to liana (11.57% and 12.96% respectively). All species

also occupied other habitat types but at far lower frequencies (saddleback tamarins: 4.65% riverine, 2.69% tree fall gap and 0.41% open understory; squirrel monkeys: 0.27% tree fall gap; red howlers: 2.93% tree fall gap, 1.04% open understory and 0.57% liana).

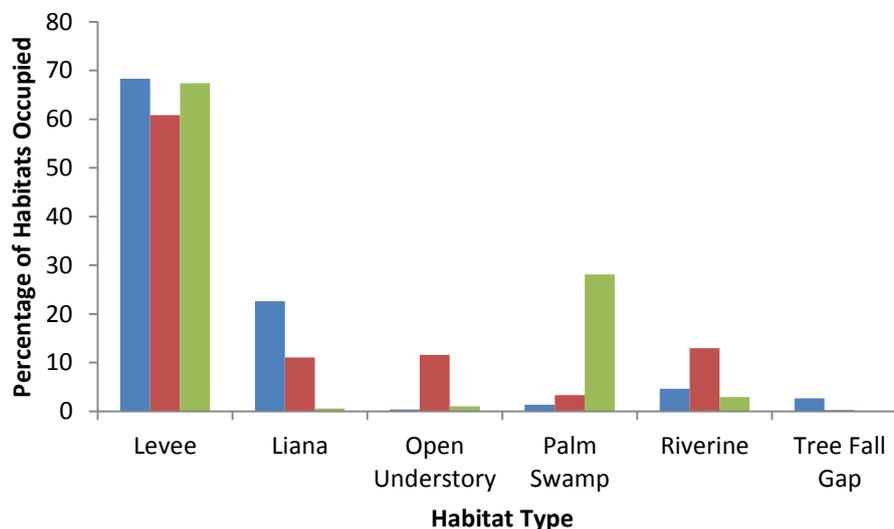


Figure 3: Habitat type occupied by saddleback tamarins, squirrel monkeys and red howlers during all behavioural observations in a study of feeding strategies in the Pacaya-Samiria Reserve, Peru in 2012

Following this, further analysis was conducted to investigate whether there was a difference in the habitat types occupied by the three species when feeding (Fig. 4.). The number of observations when feeding varied more considerably, most accounting for squirrel monkeys (n=374), with saddleback tamarins and red howlers being observed to a far less extent (n=68 and n=26 respectively). The habitat types occupied when feeding differed significantly between the three different species ($\chi^2=104.035$, d.f.=6, $p<0.005$). In order to conduct the chi-squared test, any categories that gave a value below five had to be removed. This resulted in palm swamp and tree fall gap habitats being excluded from the statistical test. As these habitats were rarely occupied by either species, this was not likely to impact the chi-squared results. The greatest overlap between all three species was in levee habitats. This was the only habitat red howlers were observed feeding in (100%). Saddleback tamarins and squirrel monkeys both occupied levees at similar frequencies (48.53% and 64.17% respectively). Apart from this overlap, saddleback tamarins also frequently occupied liana habitats (38.24%), however squirrel monkeys were observed there less frequently (9.09%). The other habitats utilised by saddleback tamarins were evenly distributed between open understory, riverine and tree fall gap (each at 4.41%). Conversely, squirrel monkeys utilised a variety of habitats at differing frequencies (10.96% riverine, 9.09% liana, 3.48% palm swamp and 0.27% tree fall gap).

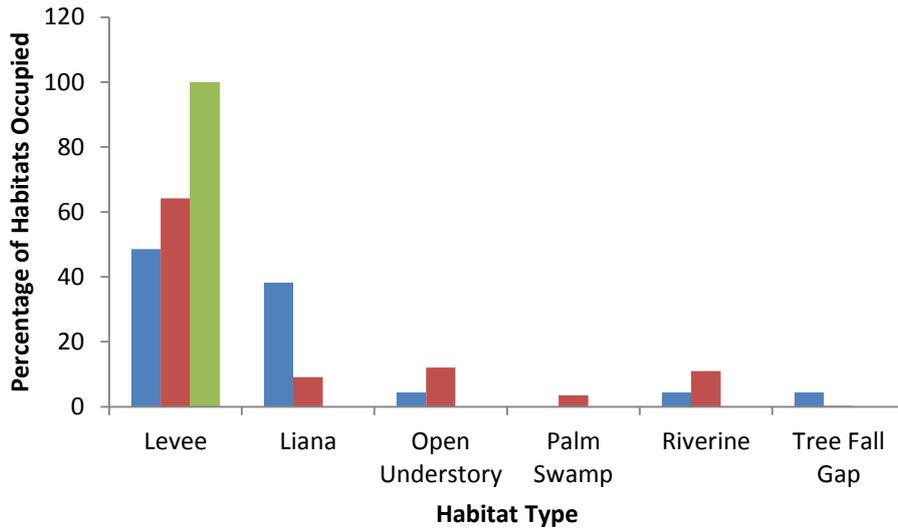


Figure 4: Habitat type occupied by ■ saddleback tamarins, ■ squirrel monkeys and ■ red howlers when feeding was observed during study of feeding strategies in the Pacaya-Samiria Reserve, Peru in 2012

Diet Composition

The diet composition of saddleback tamarins and squirrel monkeys demonstrated the most overlap, however neither showed similarities with red howlers (Fig. 5). Squirrel monkeys were observed feeding at the highest frequency (n=374) compared to saddleback tamarins (n=68) and red howlers (n=26). Red howlers were found to only consume young leaves (100%). This, in addition to the fact there were only 26 observations for red howlers, meant they were not included in the statistical tests, as it was evident that they had a significantly different diet to the other two species. Overall, the diet composition of saddleback tamarins and squirrel monkeys differed significantly ($\chi^2=13.854$, d.f.=2, $p<0.005$). To enable the chi-squared test to be conducted, any values below five were removed. As this involved very few data points this did not impact the overall results. The greatest proportion of the saddleback tamarin and squirrel monkey diets comprised of insects (55.88% and 52.67% respectively). Saddleback tamarins supplemented their insectivorous diet with more fruit (32.35%) than flowers (7.35%). However the reverse was observed in squirrel monkeys, with fruit accounting for 18.18% and flowers 28.07%. The other component of the saddleback tamarin diet consisted of 2.94% other foods, classified as gums and seeds. Squirrel monkeys instead included 0.80% of mature leaves in their diet.

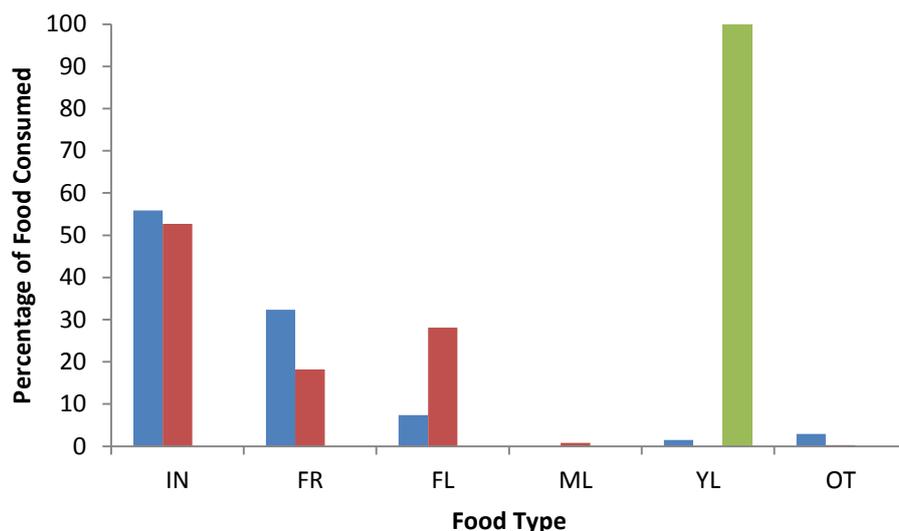


Figure 5: Food type consumed by ■ saddleback tamarins, ■ squirrel monkeys and ■ red howlers during study of feeding strategies in the Pacaya-Samiria Reserve, Peru in 2012 (IN, insects; FR, fruits; FL, flowers; ML, mature leaves; YL, young leaves; OT, other)

Comparison Data from 2011

Data collected by Operation Wallacea in 2011 at the same research site, adhering to the same methods as this study, was also available. Since diet is the key component in determining the feeding strategies of primates, the diet composition of the three species in 2011 was also analysed (Fig. 6.). The number of feeding observations were higher in 2011 for squirrel monkeys (n=450), saddleback tamarins (n=256) and red howlers (n=182). The overall diet composition differed significantly between the three different species in 2011 ($\chi^2=774.978$, d.f.=8, $p<0.005$). This data was then compared to 2012, which revealed some interesting results. In 2011, red howlers demonstrated a more varied diet, consisting primarily of mature leaves (58.79%) in addition to young leaves (28.02%) and fruits (13.19%). This was significantly different in comparison to their diet composition in 2012 ($\chi^2=42.075$, d.f.=1, $p<0.005$). Since red howlers were never observed feeding on insect, flowers or other foods, these categories were removed from the statistical test. As the fruit category had values lower than five, this also had to be excluded. This was a small amount in relation to the total number of observations, therefore should not have affected the chi-squared result. Saddleback tamarins diet primarily consisted of fruits (69.8%), supplemented by insects (23.92%) and other foods (6.27%). This was statistically different to the diet of saddleback tamarins in 2012 ($\chi^2=32.230$, d.f.=2, $p<0.005$). Since the categories flowers, mature leaves and young leaves gave values below five they had to be removed from the statistical analysis. As the sample size for 2012 data was very small (n=68), this may have affected the results. In squirrel monkeys insects accounted for 58.89% of their diet but fruits only 32.67%. They supplemented this with 4.89% young leaves and 3.56% flowers. The diet of squirrel monkeys in 2011 was statistically different to those in 2012 ($\chi^2=110.895$, d.f.=3, $p<0.005$). Categories below five included mature leaves and young leaves. Due to the large sample size for squirrel monkeys, this did not affect the chi-squared results.

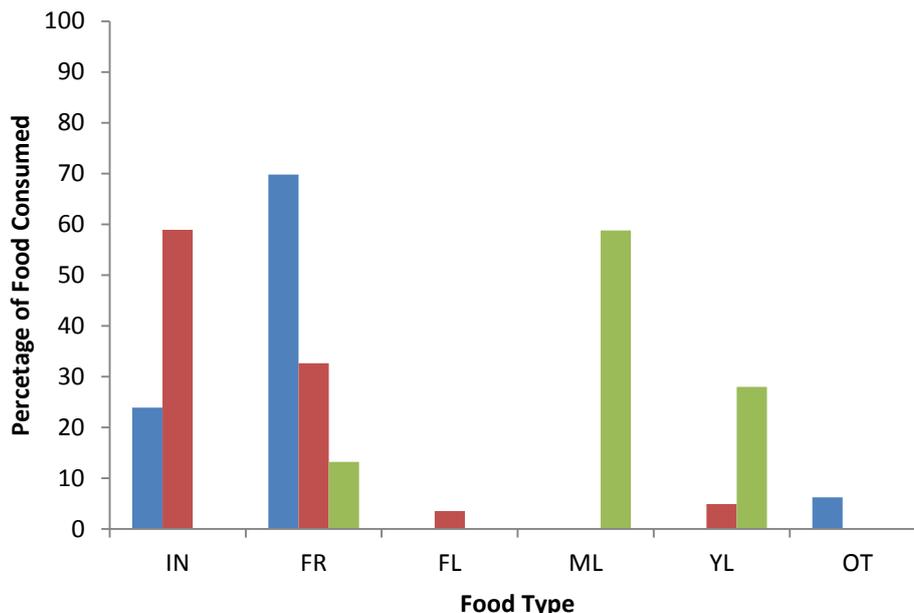


Figure 6: Food type consumed by ■ saddleback tamarins, ■ squirrel monkeys and ■ red howlers during study of feeding strategies in the Pacaya-Samiria Reserve, Peru in 2011 (IN, insects; FR, fruits; FL, flowers; ML, mature leaves; YL, young leaves; OT, other)

Discussion

Importance of Habitats in Feeding Strategies

The habitat types used during the observation of all behaviours, and purely when feeding, were found to differ significantly between all three species. One limitation of the study was that flooding in the wet season of 2012 was higher than usual, meaning there was increased flooded forest in the dry season compared to previous years. Consequently, during some periods of data collection some habitats were inaccessible to the researchers, and therefore may have resulted in bias towards some habitat types in which the primates were observed. Levees were the only habitat in which red howlers were observed feeding. Other studies have shown red howlers to occupy different forest types in proportion to their availability (Gómez-Posanda *et al.*, 2007). For example, they found that the primates used the feeding trees for a short time in mature forests, which had an abundance of food available, moving through them in a few days. This differed in areas of plantation where food resources were more dispersed, and red howlers spent several days at just one fruiting tree until the crop was exhausted, before moving to the next tree. Unfortunately day range could not be measured in the current study. This was because individual troops could not be identified, and therefore the observation times varied greatly due to the process of locating the target species each day. However other studies have found that red howlers travel the least mean daily distance in comparison with other primates (Stevenson *et al.*, 2000). This is thought to be a reflection of their use of leaves, a low quality resource that is widely distributed (Gómez-Posanda *et al.*, 2007).

Squirrel monkeys were observed in levees and lianas at the greatest frequency during all behaviours and also purely when feeding. Other studies of this species

have shown that they prefer primary forests, spending the majority of time in the understory to avoid aerial predators (Zimbler-Delorenzo and Stone, 2011). They have been shown to have day ranges of 2-5km, which is much larger than red howlers. As food availability is affected by seasonality, squirrel monkeys have been observed to increase their day range and include habitats such as flooded forests when there is decreased fruit abundance. However, much variation has been recorded both between and within different subspecies of squirrel monkeys. Studies on Brazilian squirrel monkeys have found that they adopt time minimising strategies during periods of food shortages, with troops concentrating on specific habitats in their normal range that have an increased abundance of arthropods (Stone, 2007). Conversely, Peruvian squirrel monkeys have been shown to travel further during dry seasons in order to utilise fig trees, which are a staple resources at this time of year (Stone, 2007). Some species of squirrel monkeys form associations with capuchins. Although these have smaller home ranges, they have a better knowledge of fruiting trees, which the squirrel monkeys take advantage of, especially during the dry season (Porter and Garber, 2007).

Saddleback tamarins, like the other two species in this study, occupied levees as their main habitat during all behaviours in addition to when only feeding. However, compared to red howlers and squirrel monkeys, they demonstrated the greatest diversity of habitats, as they also utilised liana, open understory and riverine habitats, each at similar frequencies. Other studies have found saddleback tamarins to more frequently utilise liana habitats and often spend time in the understory canopy (Youlatos, 2004). Heymann *et al.* (2000) likewise observed saddleback tamarins foraging predominantly in the tree trunks of the lower canopy and leaf litter, however they moved higher up in the canopy to consume the food due to the risk of terrestrial predators. Similarly to red howlers and squirrel monkeys, the home range of saddleback tamarins have also been shown to change depending on the season, with daily distance travelled ranging from 211m in the early wet season to 410m in the late wet season (Culot *et al.*, 2010). Although this study found a significant difference between the habitats used by each species, data collection occurred over a period of just two months. Therefore a longer study that includes both seasonal periods would provide an improved representation of habitat use by the primates.

Diet Composition

Overall the diet composition was found to differ significantly between the three different species. The diet of red howlers was found to predominantly consist of leaves, a category that was rarely consumed by either saddleback tamarins or squirrel monkeys. One of the limitations of the study was that the red howlers were located high in the canopy and were often obscured behind leaves, making it difficult to determine when they were feeding and if so, what food item was being consumed. Despite the small sample size of feeding observations for red howlers in this study (n=26), the results suggest this species are primarily folivorous, which is consistent with the findings of other studies. Stevenson *et al.* (2000) found red howlers to consume more vegetative parts compared the diets of several different species of primates, which preferred fruits and insects. Agostini *et al.* (2010) found the diet of species of howlers to consist of 62-64% leaves and 19-24% fruits with young leaves preferred over mature leaves, since the former contain a higher protein to fibre ratio, making them easier to digest. Moreover, young leaves contain fewer plant secondary metabolites and thus a greater amount can be consumed without the threat of any

associated negative effects (Felton *et al.*, 2009). However during the dry season where less fruit was available there was an increase in consumption of mature leaves (Agostini *et al.*, 2010). The morphological adaptations that allow red howlers to digest leaves is one of the key features that provides niche separation between them and the other sympatric species of this study (Kamilar and Pokempner, 2008).

In comparison to red howlers, saddleback tamarins and squirrel monkeys have more similarities, meaning they are more likely to experience interspecific competition. Both are relatively small Neotropical primates and therefore require less quantities of food than howlers, but this must be of a higher energy value (Kamilar and Pokempner, 2008). Since fruits and insects are easy to digest and provide high protein and energy levels, these species have been shown to adopt a frugivore-insectivore diet. This study demonstrated saddleback tamarins and squirrel monkeys to consume a similar frequency of insects (55.88% and 52.67% respectively). However saddleback tamarins supplemented this with more fruits (32.35%) and squirrel monkeys with more flowers (28.07%). Other studies have found the different subspecies of squirrel monkeys to differ in their diet compositions, but they generally spend a larger proportion of time foraging for insects (70-80%) compared to saddleback tamarins (50%) (Zimmler-Delorenzo and Stone, 2011). The foraging strategies of both these species have been observed to change with season and consequent food availability. Again, the methods in which this is achieved in squirrel monkeys varies between subspecies, however the general trend observed is an increase in dietary flexibility, with a greater consumption of insects, flowers and exudates to replace the reduced availability of fruits (Stone, 2007). Studies have also shown saddleback tamarins to adopt this strategy, increasing the use of insects and exudates by up to 21% (Nadjafzadeh and Heymann, 2008).

Since saddleback tamarins and squirrel monkeys display overlaps in some aspects of diet and habitat use, it is expected that they should demonstrate differences in their foraging strategies to avoid interspecific competition. Due to the troops in this study not being fully habituated, it was difficult to get close to the primates and therefore the exact foraging techniques could not be recorded. Also, this made it difficult to identify the exact food items being consumed and therefore limited the comparisons and consequential determination of niche separation between these two species. However previous studies have shown saddleback tamarins to forage intensively in leaf litter and manually probe closed microhabitats for prey, which is aided by the adaptations of elongated, slender hands (Smith, 2000; Nadjafzadeh and Heymann, 2008). Furthermore, this species have been found to focus around 10.1% of their foraging time on animal prey, such as reptiles (Heymann *et al.*, 2000). They attacked the head of vertebrate prey, using a cranio-cervial bite causing immediate immobilisation and prevention of the insect's escape, therefore increasing the prey capture success rate (Heymann *et al.*, 2000). Conversely, squirrel monkeys have large molars and premolars with thick enamel, which they use to crunch branch ends and acquire the insects inside, and are able to obtain insects hidden in tree trunks with the use of their pseudo-opposable thumbs (Rosenberger, 1992). Although this study was unable to identify specific species of food items consumed, the overall diet composition was found to be statistically different between the species of primates, therefore indicating the use of different food types may facilitate niche separation.

Comparison Data from 2011

Comparison of diet composition revealed a statistical difference within each species between 2011 and 2012. Red howlers were observed to have a more varied diet in 2011 compared to 2012. However as mentioned previously, the sample size of red howler feeding data collected in 2012 was very small, and therefore this may have skewed the results. Some primate species have been observed to conduct vocalisations subsequent to bouts of feeding (Sueur *et al.*, 2011). As red howlers could often only be located via following their vocalisations, this was likely to be the reason why so little feeding data was collected. Large differences were also observed for both saddleback tamarins and squirrel monkeys between 2011 and 2012. One explanation for this could perhaps be due to changes in the climate across the two years. The rainfall in the wet season of 2012 was much greater than in 2011, giving rise to higher levels of flooded forest (Bodmer *et al.*, 2012). Although studies have yet to show primates to be directly affected by changes in flooding, if severe fluctuations in seasonal flooding continue, this may change. Tree growth and reproduction are affected by climate and some species of plant may not be able to survive the increased periods of severe flooding that the rainforests are becoming subjected to (Grogan and Schulze, 2011; Bodmer *et al.*, 2012). Such circumstances may result in a reduction in the food resources available to the primates, causing adverse impacts on their feeding strategies. Furthermore, flooding reduces the proportion of land available to terrestrial animals, forcing them to move to habitats such as levees during the wet season (Bodmer *et al.*, 2012). This could have a consequential effect on the food chain in the rainforest. A decrease in the spatial distribution between predators and prey would result in an increase in predator abundance in the subsequent year (Polis *et al.*, 1997). An increase in terrestrial predators may then impact primate populations. Although primates are often at more risk from aerial predators, terrestrial mammals such as ocelots are known to target primates (Bianchi and Mendes, 2007; Abreu *et al.*, 2008). Considering the results of this study revealed all three primate species to occupy levee habitats across all behaviours at the highest frequency, and most notably when feeding, the increased occupation of this habitat by terrestrial animals suggests the primates may be more vulnerable to terrestrial predators if such severe seasonal flooding continues. Therefore changes in climate could not only indirectly disrupt future populations of primates, but also impact their feeding strategies.

The results from this study gave rise to several factors that would be interesting to research further. Although there was a statistical difference in the habitat types occupied between saddleback tamarins, squirrel monkeys and red howlers there was a large overlap between all three species in levees. Further research involving the identification of the specific tree species occupied by the primates would provide an indication as to whether there is further niche separation between species within habitats. Moreover, the identification of plant species would enable more specific food items, such as fruits, leaves and flowers, to be identified. This would improve the quality of data collected on diet composition, and again allow for deeper analysis of the niche separation between the primates. One of the most interesting findings of this study was the differences in diet within species across 2011 and 2012. Since there is an interannual time scale on which rainfall fluctuates, it is difficult to predict the future climate changes that may occur in the Amazon. However, long term monitoring of wildlife populations in relation to changes in climate will enable any

impacts on primates and their feeding strategies to be revealed. In response to this, it would be valuable to conduct further studies, in which changes in climate are compared to primate populations within a specific area. This would help determine whether decreased land availability, due to increased rainfall and therefore flooded forest, impact predator and prey ratios, and whether this affects primate populations. Changes in climate could also be analysed in comparison with the diet of primates to determine whether this impacts their feeding strategies. The collection of such data from primates in a protected reserve would also provide vital information that could be applied to protect primates in other locations.

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