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# Effects of Re-Grown Forest Habitat on Lemur Catta Behavior

Sophie Ackoff  
*SIT Study Abroad*

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# Effects of Re-grown Forest Habitat on *Lemur catta* Behavior



Sophie Ackoff

Fall 2009

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## **ABSTRACT**

*This study examines the effects of re-grown forest habitat on *L. catta* behavior at Berenty Private Reserve in Southern Madagascar during the early wet season. Evaluation of the reforested area versus natural forest revealed significant differences in species composition and food availability. Though the re-grown forest showed signs of forest regeneration and total greater food availability, the natural forest of Malaza proved to contain more preferred food sources for *L. catta*. Behavioral observations were collected over eight full-day troop follows and showed significant differences in feeding behavior, activity budget, and intra-troop and inter-troop aggressions. The WELL troop in Ankoba, the re-grown forest, experienced a greater percentage of time spent moving and feeding in search of quality food products, less time resting, heightened levels of intra-troop competition, and a larger home-range. CX troop in Malaza benefited from an abundance of native species with high food-availability, such as *Tamarindus indica* and *Rinorea greveana*. Despite disparities in behavior between the groups, the re-grown forest of Ankoba is successful in supporting lemur populations. Reforestation, if done correctly and with special regard to introduced species, is a conservation strategy necessary for the island of Madagascar.*

## **INTRODUCTION**

Madagascar's native biodiversity is highly threatened by the degradation and loss of its natural habitat. The habitat of *Lemur catta*, the

island's flagship species, is threatened due to conversion of forest for charcoal production, extensive grazing by cattle and goats, fires, and slash-and-burn agriculture. (Ralison, 2006) The south of Madagascar is of special concern for conservation efforts because of its underrepresentation in the amount of its protected areas. Habitat destruction is the main threat to the lemurs of southern Madagascar and studies have shown that lemur diversity in the south is the lowest in the country. (Fenn et. al., 1999; Goodman et. al., 2002) Reforestation is a proposed conservation strategy to preserve native flora and fauna. This study seeks to examine the effects of a re-grown forest on *Lemur catta* behavior in the Berenty Private Reserve in the south of Madagascar.

## **BACKGROUND**

### ***Lemur catta***

*Lemur catta*, or the Ring-Tailed Lemur, is a diurnal lemur species that is the most terrestrial of all lemurs and also the most extensively studied (Jolly, 2004). Its range is limited to southern Madagascar and the species depends on riparian, gallery forest and dense euphorbia bush. (Sauther, 1998) *L. catta* are ecological generalists that exhibit physiological and behavioral plasticity to adapt to a range of habitats. This plasticity increases their ability to adapt to ever increasingly degraded habitats. (Elwanger, 2002) However, the species is listed as an IUCN Red-listed, vulnerable species and experiences habitat loss due to human activity. (Ganzhorn, 2008) *L. catta* live in multi-male groups, ranging from 5-27 individuals, with approximately 1:1 sex ratios

(Sussman, 1977). Adult females are dominant over males and occupy the highest rank in the dominance hierarchy. (Jolly, 1966) This female dominance is suggested to have evolved as a response to the high costs of reproduction, requiring females to have access to valuable resources in seasonally harsh environments. (Pride, 2005; Sauther, 1998) *L. catta* are opportunistically omnivorous, but their feeding is focused on ripe and unripe fruits, young and mature leaves, leaf stems, and seeds. (Jolly, 1966; Sussman, 1977) *L. catta* are highly dependent on specific food sources and their feeding ecology is finely tuned to the seasonal nature of these resources. (Sauther, 1998) The abundantly distributed *Tamarindus indica* provides one of the most important sources of food for *L. catta* throughout the year. (Jolly et. al., 2002)

## **Berenty**

Berenty Reserve is a 240-hectare private reserve along the Mandrare River in southern Madagascar. It consists of four distinctive areas: Ankoba, a largely re-grown gallery forest including non-native trees grown from cleared ground; a tourist front along the western boundary; Malaza, a natural gallery forest with a canopy cover greater than 50 percent; and a scrub forest with more than 50 percent open sky. (Koyama, 2002) The closed-canopy gallery forest is dominated by *Tamarindus indica*, *Rinorea greveana*, *Acacia*, and *Celtis* trees. The scrub, or spiny, forest consists of a dense underbrush with *Tamarindus indica*, *Acacia*, *Euphorbia*, and *Alluaudia* trees. An open hotel garden with exotic ornamental vegetation and many native species is not far from Malaza. Berenty has been the site of lemur research since the early

1960's when Alison Jolly began her pioneering studies on the behavior of *Lemur catta*. The reserve is home to three diurnal lemur species: *Lemur catta*, *Prophithecus verreauxi*, and *Eulemur fulvus rufus x collaris*. Mean group sizes for *L. catta* in each habitat are 16 individuals in the Tourist zone, 13 animals in the Gallery forest, and 9 animals in the Scrub. (Jolly et. al., 2002) The reserve is well protected from anthropogenic threats but introduced species grown in open areas supplement the diets of the lemur populations. The reserve is a center of ecotourism in the south and the lemurs are therefore habituated to humans, which facilitated observation.

At Berenty, 70 percent of annual rainfall (400/580mm) occurs between November and February, with very little rainfall between May and September. (Pride, 2005) Most years follow this predictable seasonality to which *L. catta* have adapted, however, annual rainfall and fruit abundance can vary dramatically. This leads to an intensification of environmental stresses in years of draught.

## **Malaza**

Malaza forest is a 100-hectare area composed of gallery forest, scrub, and spiny forest areas. The closed-canopy gallery forest next to the Mandrare River is the kind of riparian forest that is among the richest of *L. catta* habitats remaining. (Sussman et. al., 2003) *Tamarindus indica* is the dominant tree species in terms of basal area. (Simmen, 2003) The introduced species, *Leucocephala leucaena* was removed from the front zone in 2005 after discovery that consumption of the plant led to alopecia in lemurs, but was left



for study in the north end of Ankoba. There are no introduced species within Malaza, but lemur troops based in Malaza feed on fruits and flowers of introduced species outside the forest, especially during the dry season.

(Soma, 2006)

## **Ankoba**

In the 1950's the owners of Berenty, the de Heaulme family, replanted trees in a 40-hectare area called Ankoba because the land was not found suitable for a sisal nursery. (Rambeloarivony dissertation 2009; Jolly, 2006) The land was initially cleared for Tandroy local farms around the time of the de Healmes arrival to Berenty. Original *Tamarindus indica* trees remain in the forest because neither local people nor the de Heaulme's cleared them. (Jolly, 2006) *Pithecellobium dulce*, an introduced species, was planted along with native species including *Rinorea greveana*. *P. dulce* is reportedly an excellent food source for lemurs due to its protein-rich flowers and pods. Its nurse trees shelter wild seedlings distributed by lemurs unlike *T. indica* which inhibit seedlings. (Jolly, 2006) A drainage system ensures water provision and one of the Reserve's main water wells is located within the forest. Planted over fifty years ago, the area is now considered an old second-growth forest. (Jolly et al. 2006) The forest supports 500 *L. catta* per square kilometer. (Jolly, 2006) Troops based in the forest make excursions out of their territories to consume introduced species planted in the garden to the north and open areas containing such introduced species as *Azadirachta indica*. No research has been conducted to examine structural diversity and phenology of the

planted forest and no comparative studies between the natural forest and modified environment have been performed. This is the first study to compare the two habitats in terms of their effects on *L. catta* behavior. Anthropogenic factors affecting Ankoba other than introduced species include the well, water troughs, the presence of a forest manager who lives within WELL's territory, tourist traffic, and village fields within range of forest troops.

## **METHODS**

This study reflects 97.37 hours of behavioral observation of two *Lemur catta* troops. Fieldwork at the Berenty Private Reserve was conducted during the early wet season from November 1<sup>st</sup> to November 20<sup>th</sup>. One day was dedicated to training and troop selection; one day was required for an evaluation of food availability and plant species composition in each habitat; and the remaining 16 days were available for the collection of behavioral data.

### **Troop and Site Selection**

To study the effects of re-grown forested habitat on *Lemur catta* behavior, two troops were selected for comparison: one troop occupying a territory in the natural forest of Malaza and one troop occupying a territory in the reforested area of Ankoba. Small groups were selected to make complete scan survey counts more feasible. Troop WELL, named because of the presence of a functional well in the heart of its territory, was chosen as the Ankoba group because of its small size. Studies show an average group size

of 12–16 non-infant animals (four–six adult females) at Berenty Reserve, with groups tending to fission when they exceed 20–25 animals (Jolly et al., 2002; Koyama et al., 2002). The group is composed of eight individuals: three adult females, two adult males, one sub adult female, one sub adult male and one juvenile male. One infant was present but not counted in scan surveys. CX was selected as the troop from Malaza forest due to its similarly small size. Because group size has been shown to affect vigilance behavior and feeding agonism, troops were chosen to be the most similar size possible. (Sauther 1993; 2002) CX is composed of six individuals: three adult females, one adult male, and two sub adult females. There were three infants at the start of observations, but only two at its conclusion. The slight difference in group size (6 versus 8 individuals) should have no significant effect on the results of the study, due to the short period of observation.

*Lemur catta* was chosen from the three diurnal lemur species at Berenty for this study because of the extensiveness of research that has been conducted on the species at the reserve since the 1960s. This knowledge base is helpful for reference when examining how a particular environment, in this case a reforested one, can affect behavior.

### **Behavioral Observations**

The behavioral data analyzed in this study is compiled from eight full-day troop follows: four days with each troop. At the start of the study, 16 days of six hour, half-day observations were planned but due to difficulties finding the troops at midday, full day follows were initiated and the full eight days

were able to be completed. Therefore, behavioral data of the WELL troop consists of four days of half day observations. For the remaining follows, data collection began as soon as the troop was found each morning, ideally at 6h00 and the troop was followed until 18h00. If the troop was not located before 7h30 then the follow was abandoned for that day. In total, WELL was observed for 52.45 hours, of which 48.95 hours were used for analysis, and CX was observed for 44.92 hours.

I employed the scan survey method for group sampling to quantify activity budget and feeding behavior. I chose to do scan survey as opposed to focal animal observation because I wanted to examine behavioral disparities on a troop level. A scan was taken every five minutes and the instantaneous behavior of each individual was recorded as Feeding, Moving, Traveling, Individual Grooming, Mutual Grooming, Resting, Sleeping or Sunning. The behavior was not recorded for an individual if they could not be seen within thirty seconds. Because no distinction was made between foraging and feeding, the word "feeding" in this study refers to both. "Moving" was defined as movement within a tree, whereas "traveling" was directional movement among trees or on the ground with tail raised. If an individual remained stationary with its eyes open then it was considered "resting" and was considered "sleeping" if the eyes were closed.

Several aspects of feeding behavior were noted. At each scan, the food species, if known, was recorded. The plant part exploited was recorded as green fruit, ripe fruit, new leaves, leaf buds, mature leaves, or flowers. The

height of the lemur in the tree during feeding was noted based on a scale of 0-5, specified as follows:

Height of Lemur in Tree

Score	Height in Meters
0	0
1	1-5
2	5-10
3	10-15
4	15-20
5	20+

In addition, the part of tree, or forest site, where the lemur fed was recorded as ground, trunk, major branches, or crown. Finally, a tally was kept to determine total number of patches exploited per day. If an individual was feeding in a patch previously unexploited that day during a scan, the patch was counted. One patch is defined as a single tree, bush, vine, cactus, or decaying log fed on by the troop.

All antagonistic and affiliative social behaviors were recorded ad libitum as they occurred throughout the day. These included all intra-group, inter-group, and inter-species encounters. Every time two troops came within 10m of one another it was recorded as an encounter. For each encounter, the time, the species involved, whether the encounter was peaceful or aggressive, any food species involved, and whether there was a winner or the encounter resulted in a draw was noted. Spats, the submissive call used to infer dominance relationships (Inchino, 2006) were tallied and classified as

either related to feeding or unrelated to feeding. Lastly, all scent markings were recorded as genital or wrist markings.

To determine distance traveled per day and total home range area, the location of the troop was recorded every time the troop relocated. A map of Berenty with a twenty-five by twenty-five meter grid was used to identify the location of the troop in the forest. Location of inter-troop encounters were noted especially as their outcomes determined the limits of the troops' home range.

### **Habitat Evaluation**

In order to study the effects of a re-grown forest habitat on a lemur species, it is essential to assess how the re-grown forest differs from the natural forest. Two transects were taken to examine tree species composition and food availability. The transects were chosen at random within the troop's home range and measured two meters by eighty meters. Along each transect, the species, height, crown diameter, and DBH (diameter at breast height) were taken for each tree that exceeded 5cm DBH. For trees with multiple trunks, the sum of all of the trunks was used to evaluate DBH. In addition, all small trees and saplings were counted. Small trees were defined as trees with a DBH less than 5cm but a height of greater than 50cm. Saplings were defined trees with a height of less than 50cm. Height measurements were estimated using the same scale as feeding height. For comparing the

average crown diameter, a more sensitive height scale was used to account for smaller differences in crown diameter than tree height.

#### Crown Diameter Length

Score	Height in Meters
0	0
1	1-2
2	2-5
3	5-10
4	10-15

To evaluate food availability, a phenological assessment was conducted on the five most common tree species. A random sample of five trees of each species was taken and the percent cover of old leaves, new leaves and buds, mature leaves, fruits, and flowers was estimated using the following scale:

#### Percent Cover of Food Source

Score	Percent Cover
0	0
1	1-25
2	25-50
3	50-75
4	75-100

### **Data Analysis**

To analyze scan survey data, the number of individuals engaging in each activity was added every 30 minutes and as a daily total. These sums were then expressed as a percentage of total scan survey counts. One scan

survey count is defined as the observation of one individual during one scan. To find the percentage of time the group as a whole spent engaging in each activity (Feeding, Moving, Traveling, etc.) per half hour, the total number of scan survey counts for each activity was divided by the total number of scans for that half hour. In thirty minutes there are a total of six scans (one scan every five minutes.) If, for example, in WELL, all of the individuals' activities were recorded every five minutes for thirty minutes, eight individuals times six scans would equal a total of 48 possible scan survey counts. If there were 16 individuals were feeding during those scans, then the percentage feeding for that half hour would be 16 divided by 48, or 33 percent. Daily totals were then assessed by taking the averages from each half hour. Activity budget, diet composition, distance traveled, and social behaviors were averaged for each group daily and as a total study average. Standard deviations and variance levels were determined and two-tailed T-tests were used to assess significance. Disparities in data were deemed significant if the p value was less than or equal to .05.

For comparing average daily activity budget, certain activities were grouped together such as: resting and sleeping, moving and traveling, and individual and mutual grooming. For additional analysis, percentage of time spent as active versus inactive was determined. Active behaviors include moving, traveling, and feeding whereas inactive behaviors include grooming, resting, sleeping, and sunning. Daily totals of diet composition, part of tree exploited, and height in tree at feeding were averaged for each troop for



each day and as a study total. Calculations to determine daily averages of placement in tree during feeding (ground, trunk, major branch, or crown) were not made because of inconsistencies in data collection. Average percentage of feeding each half hour throughout the day was determined to show daily feeding patterns. This was also done compositely for sleeping and resting to show daily resting patterns. Analysis began starting from 7h00 since data from 6h00 to 7h00 was not available for all days. Number of patches exploited per day was analyzed in addition to average time spent feeding per patch. I found this value by dividing the total feeding scan counts per day by the number of patches exploited per day.

For social behaviors, the total number of food-related spats per day was divided by total number of feeding scans to compare food-related spats per feeding time among the two troops. The average was then taken. The total number of feeding scan counts was calculated starting from 7h00 since data was not available from 6h00 to 7h00 for all days. The number of food-related spats was also divided by total number of feeding hours as another method to show spats per feeding time. If at least ten percent of individuals were feeding during that hour it was considered a feeding hour. For comparing rates of intra-troop aggression, the number of spats was used.

The number of scent marks for each troop was averaged daily and as a study total. To eliminate the effect of differing troop size on comparison, the average was divided by number of individuals to find average number of scent marks per individual. Frequency of both inter-troop and interspecies

encounters was averaged per day. For further analysis, I considered the number of aggressive encounters out of the total number of encounters to find the percentage of aggressive encounters.

Daily range size was calculated using the map grid. The sum of all quadrants covered in a day was taken to calculate the total area in square meters. For the total home range area, a sum of all quadrants visited throughout the course of the study was totaled. Territorial boundaries were drawn from outcomes from inter-troop encounters when possible. Otherwise, they were assumed from location mapping during observation hours.

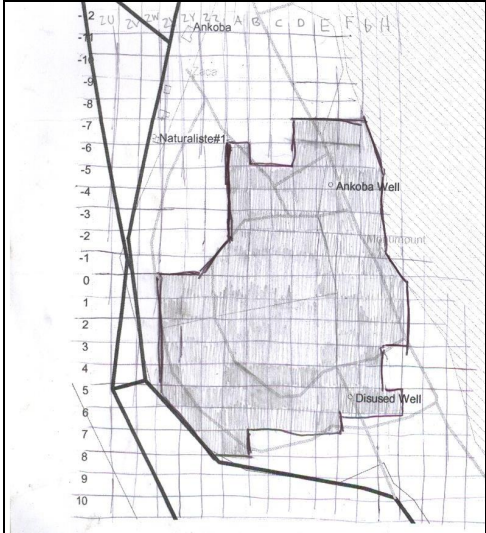
To determine food availability, I examined both fruit availability and new leaves/buds availability because of their great importance in the *Lemur catta* diet. (Mertl-Millhollel, 2003) For fruit availability, I multiplied the fruit score (which is a measure of percent coverage of the tree by fruit) of each fruiting tree species by the number of that tree species in the transect. In Ankoba, both *P. dulce*, *R. greveana*, and *Celtis philliensus* were fruiting, so the fruit availability measurement for Ankoba is a composite of these three tree species. In Malaza, *R. greveana* and *C. philliensus* were fruiting, so the fruit availability includes these two species.

## **RESULTS**

### **Home Range Determination**

The home range of the WELL troop was found to be over 3 times the size of CX home range, consisting of 73,750 square meters as opposed to CX's

home range of 18,437.5 square meters. These ranges are represented below on the grid of Berenty, divided into twenty-five by twenty-five meter quadrants. Both troops occupy territories along the Mandrare River in gallery forest habitats. The daily forest area covered by each troop was found to be significantly different. ( $p \leq .002$ ) WELL troop covered an average of 13437.375 square meters per day whereas CX troop covered an average of 4453.125 square meters.



WELL Home Range



CX Home Range

**Habitat Evaluation**

The habitat of WELL troop, Ankoba forest, was re-grown with a majority of native species but it differs markedly in vegetation density, species composition, and phenology from the habitat of CX, Malaza forest. The tables below catalog averages in height, crown diameter, and DBH for each tree species with a DBH exceeding 5cm found within a random transect for each habitat. Tree heights and crown diameters are based on a scale of 1-5.

Table 1A: Tree Abundance and Size in Transect of 160m -- Ankoba

#	SP	Density (trees/m <sup>2</sup> )	HT Average Score	CD Average Score	DBH (m)
12	<i>Pithecellobium dulce</i>	0,075	2,7	1,33	42,83
8	<i>Rinorea greveana</i>	0,05	1,75	1,25	9,125
6	<i>Celtis philliensus</i>	0,0375	2	0,833	6,58
4	<i>Tamarindus indica</i>	0,025	1,25	1	7,875
1	<i>Celtis bifida</i>	0,00625	1	1	6

Table 1B: Tree Abundance and Size in Transect 160m – Malaza

#	SP	Density (trees/m <sup>2</sup> )	HT Average Score	CD Average Score	DBH (m)
13	<i>Rinorea greveana</i>	0,08125	2	1,15	15,12
6	<i>Celtis bifida</i>	0,0375	3	1	18,33
3	<i>Crateava excelsa</i>	0,01875	3	1,33	19,5
2	<i>Celtis philliensus</i>	0,0125	2	1	7,5
1	<i>Tamarindus indica</i>	0,00625	2	1	36
1	<i>Cordia</i>	0,00625	3	1	24,5

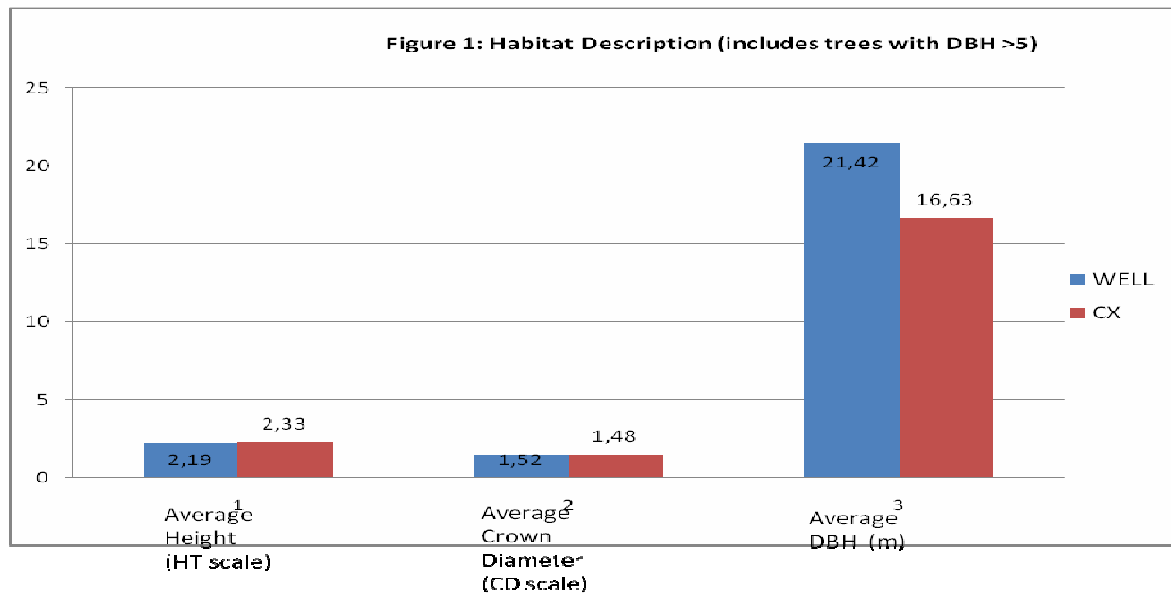
	<i>caffra</i>				
1	<i>Trycalisia</i>	0,00625	2	1	21,5

The abundance of trees with a DBH measuring greater than 5cm DBH were relatively equal in Ankoba and Malaza, 31 and 27, respectively. However, calculations of the diversity of the two habitats revealed a statistically greater diversity of tree species in the natural forest of Malaza. One introduced species, *Pithecellobium dulce*, was present in the transect of Ankoba and it proved to be the dominant tree species with a density of .075 trees per meter squared. This tree species is not present in the natural forest of Malaza. Because only trees with a DBH greater than 5m were surveyed in the transects, non-arboreal vegetative diversity was not represented.

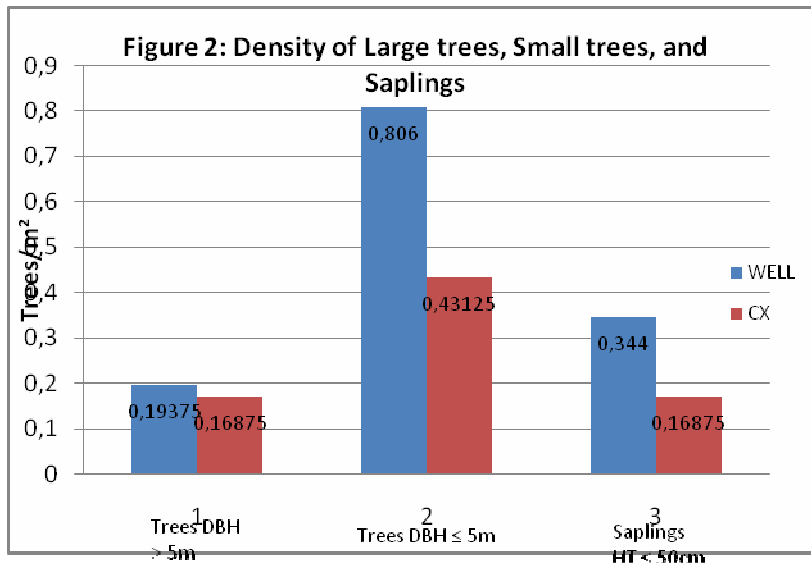
There was no significant difference found between the height and crown diameter of trees in the two habitats. The average height of trees in Ankoba was 2.19 versus 2.33 in Malaza (based on scale) which corresponds to a height of approximately 10 meters. The average crown diameter in Ankoba and Malaza was 1.2 versus 1.48, respectively, according to scale. The average DBH of trees in Ankoba was greater, but not significantly greater, than those in Malaza with an average DBH of 21.41 cm as opposed to 17.11cm.

The graph below compares these calculations between habitats. Note that because of differing scales, height, crown diameter, and DBH are not to

be compared. The graph merely compares results for each habitat for each measurement separately.



Although the density of large trees is similar between the two habitats, the density of both small trees, defined as trees with a DBH of  $\leq 5$ m, and the density of saplings, trees with a height greater than 5cm, was much greater in Ankoba. The density of saplings was twice as great in Ankoba than in Malaza and the density of small trees was almost twice as great (1.87 times greater.) This disparity in composition of old and new growth is represented in Figure 2 below. This greater density of new growth shows higher rates of regeneration in Ankoba forest. (Millhollen et. Al., 2006)



The habitat evaluation also consisted of an assessment of food availability. The tables below show the average score for all parts of the tree used as food source by *L. catta*, and therefore represent food available for consumption. Flowers were not available in either habitat range. Ankoba was found to have a greater availability of food sources when considering new leaves/buds and fruits.

Table 2A: Food Availability in Key Tree Species – Ankoba (according to scale)

Tree Species	Average score for Old leaves	Average score for New leaves/buds	Average score for Mature leaves	Average score for Fruits	Average score for Flowers
<i>Pithecellobium dulce</i>	0,8	1,2	2,8	2	0
<i>Rinorea greveana</i>	1	0,8	4	1	0
<i>Tamarindus indica</i>	0,6	2,8	2,6	0	0
<i>Celtis bifida</i>	0,2	1	1,6	0	0
<i>Celtis philliensis</i>	1,2	0,8	3,2	2	0

Table 2B: Food Availability in Key Tree Species – Malaza (according to scale)

Tree Species	Average score for Old leaves	Average score for New leaves/buds	Average score for Mature leaves	Average score for Fruits	Average score for Flowers
<i>Rinorea greveana</i>	0,6	0,6	3,6	2,4	0
<i>Tamarindus indica</i>	0,8	3	3	0	0
<i>Celtis bifida</i>	0,2	1,2	2,2	0	0
<i>Celtis philliensus</i>	1,25	1	3	1	0

*Rinorea greveana* in Malaza had a significantly greater score for fruits than the trees in Ankoba ( $p \leq .03$ ). The average scores were 2.4 and 1, respectively. A score of 2.4 is greater than 50 percent coverage whereas a score of 1 is 1-25 percent coverage. There was also a greater density of *R. greveana* in Ankoba: (0825 trees per square meter) versus .05 trees per square meter.

When considering the average fruit availability of all fruiting trees in the two habitats, it appears that Malaza has slightly higher fruit availability (average of .6 as compared to .48, according to scale.) But if the abundance of fruiting trees is taken into consideration then Ankoba forest has greater fruit availability (44 versus 33.2, according to scale.) This is a result of the introduced species *P. dulce* which was in fruit during observations and is dominant within the area. In addition, *Celtis philliensus* is found in both habitats and had greater fruit availability in Ankoba.



Disparities in new leaf and leaf bud availability proved even more significant. Using the same method as used to determine fruit availability, I determined a new score for leaf availability that accounts for abundance of leaf-covered trees. Ankoba's score was 37.8 and Malaza's score was 20. This comparison has limitations: *P. dulce* is included in the sum for Ankoba but not for Malaza because it is not present in the natural forest. However, there are other trees in Malaza forest that provide a source of leaves and leaf buds that are not included in this calculation. These trees, however, were not identified as major food sources.

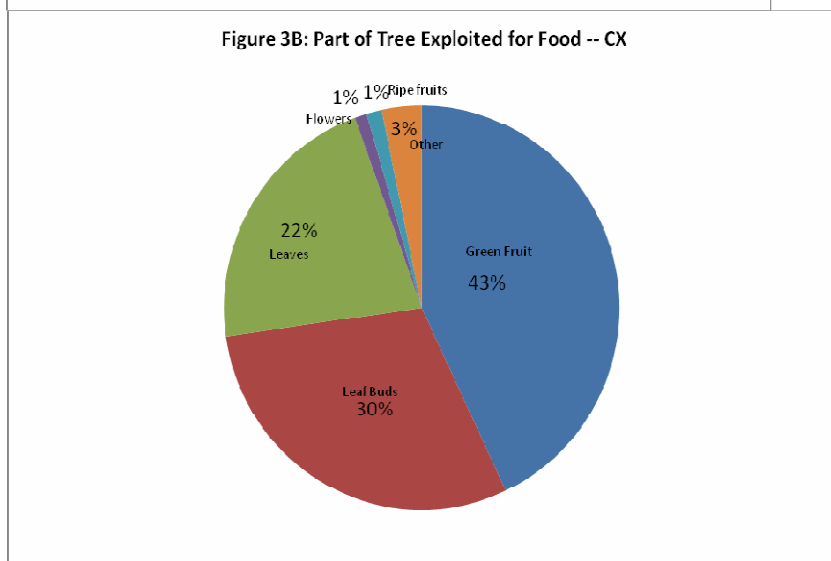
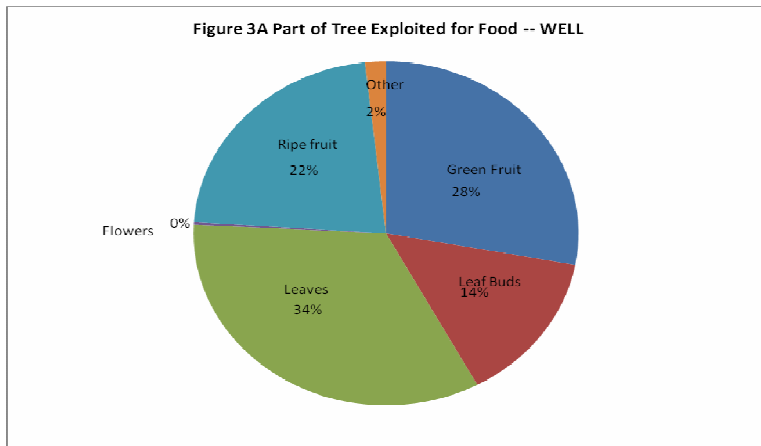
The new leaves and leaf buds of *Tamarindus Indica* are a major food source for both troops. WELL feeds from this tree 28 percent of the time whereas CX exploits it 36 percent of the time. The *T. indica* in CX home range were found to be slightly more food rich (with a score of 3 versus 2.8,) but the species was found to have a greater density in the WELL home range (.0025 trees per meter squared versus .00625 trees per meter squared in Malaza.) This contributes to Ankoba's high score for new leaf/ fruit availability.

### **Diet Composition and Feeding Behavior**

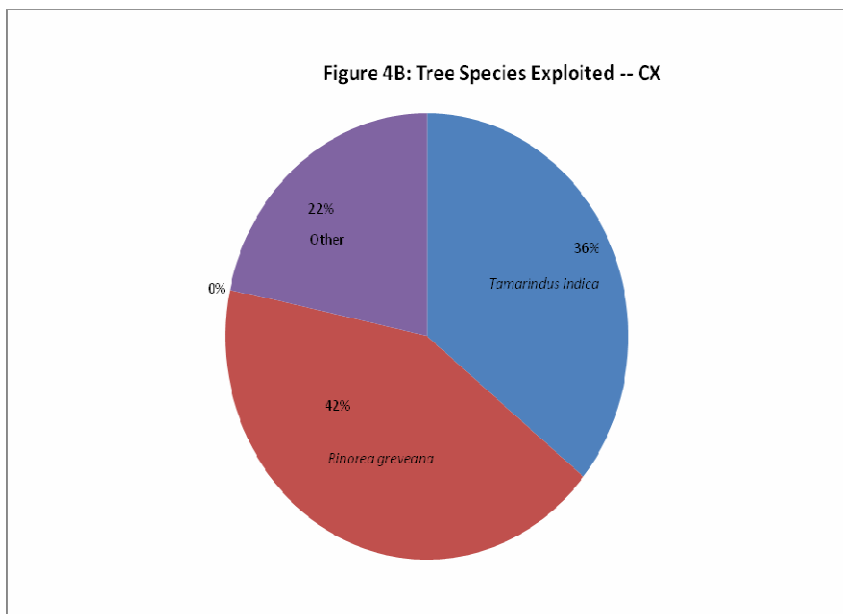
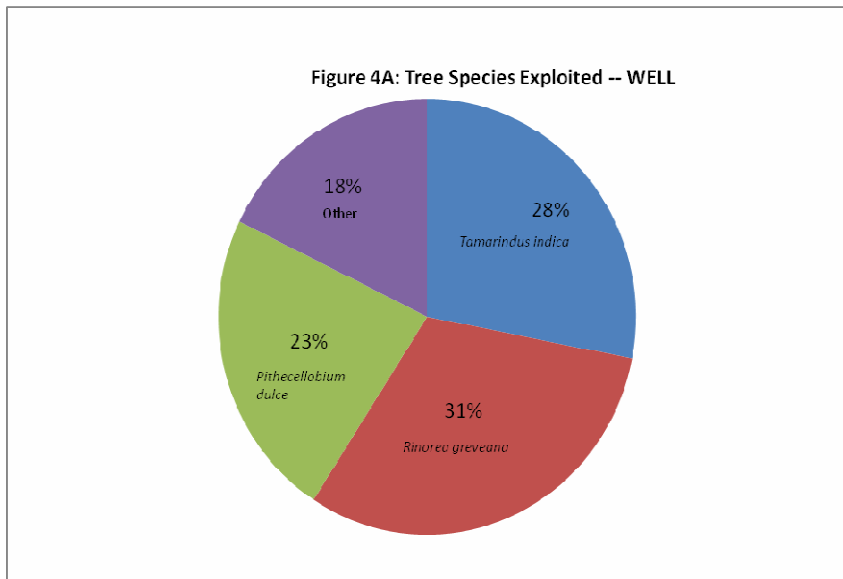
WELL exploited an average of 45.75 patches per day whereas CX exploited an average of 39.5. This disparity did not prove significant, however, especially if considering differences in group size. There is also no statistically significant difference between average time spent feeding per patch

between the troops. WELL spent an average of 6.06 feeding scans per patch whereas CX spent an average of 5.375 scans per patch.

Results reveal extensive differences in diet composition and feeding behavior between the two groups. Figure 3 below illustrates the discrepancy in percent composition of each food source in the diets of WELL and CX. CX's diet relied most heavily on green fruit (42 percent) This feeding behavior is a result of the dominance of *R. greveana* in their home range and its high availability of green fruit. (see Table 1B and Table 2B) Figure 13B shows CX's preference for *R. greveana* as a food source. The troop utilizes the tree 42 percent of the time as compared to 31 percent for WELL. As follows, WELL consumes less green fruit (29 percent of its diet.) To complement its diet, WELL eats ripe fruit available only in Ankoba. It is this introduced species, *Pithecellobium dulce*, which comprises 23 percent of their diet. Both troops' diets consisted of a substantial proportion of leaves and leaf buds, but a divergence exists in the breakdown of each particular food source. WELL consumed a diet of 34 percent leaves and 14 percent leaf buds whereas CX ate 22 percent leaves and 30 percent leaf buds. Therefore, CX consumed over twice the proportion of leaf buds as WELL. *Tamarindus indica* proved most rich in availability of leaf buds in both habitats out of all tree species present, but there were not significant differences in leaf bud availability between *T. indica* in the two habitats. CX fed from *T. indica* a greater percentage of the time and therefore its diet consisted of a greater percentage of leaf buds.

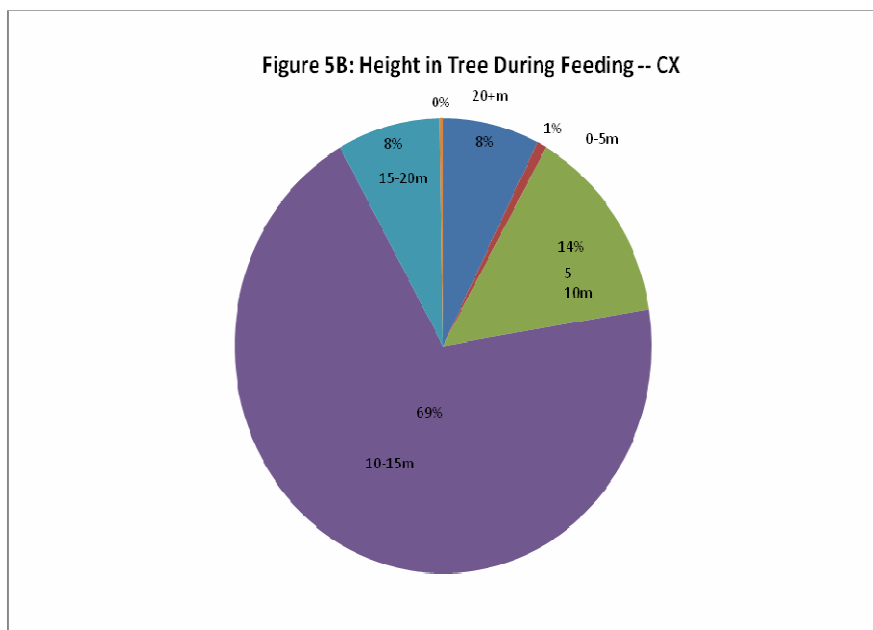
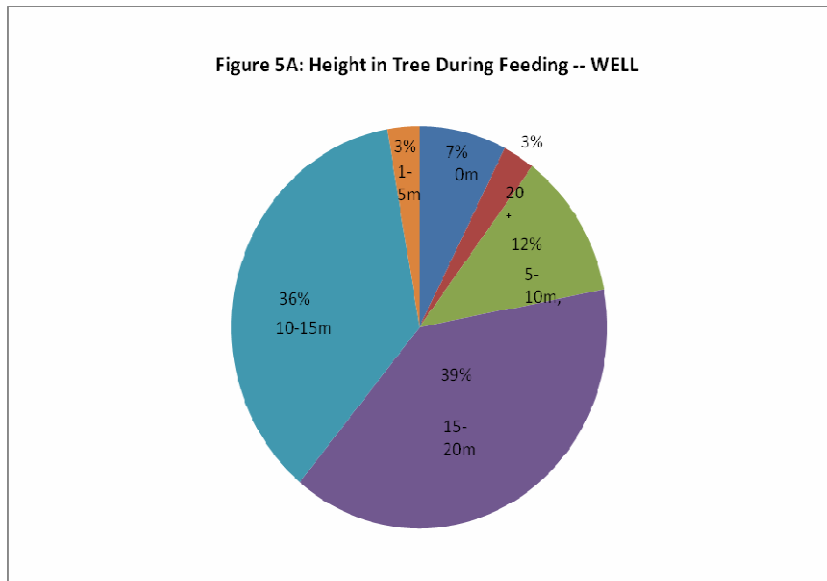


Both troops consumed minimal to no flowers because of their unavailability. Other food sources consumed include dirt, grass, decaying wood, insects, etc. *L. catta* ingest very small amounts of sandy earth as well as bark of dead wood, and exploit hollow trunks of *T. indica*, which contain old termite galleries. They occasionally ingested decaying organic matter. (Simmen, 2003) These sources comprised a minimal proportion of both WELL and CX'S diet, 2 percent and 3 percent, respectively.



Differences in feeding behavior include foraging strategies. WELL troop spent a greater proportion of their time higher in the forest canopy. 39 percent of their time was spent at a height of 15 -20m as opposed to eight percent for CX. Though there was no significant difference in average height of trees found in their home ranges, WELL fed from *P. dulce* 23 percent of the time and this tree species was observed to have typically greater heights,

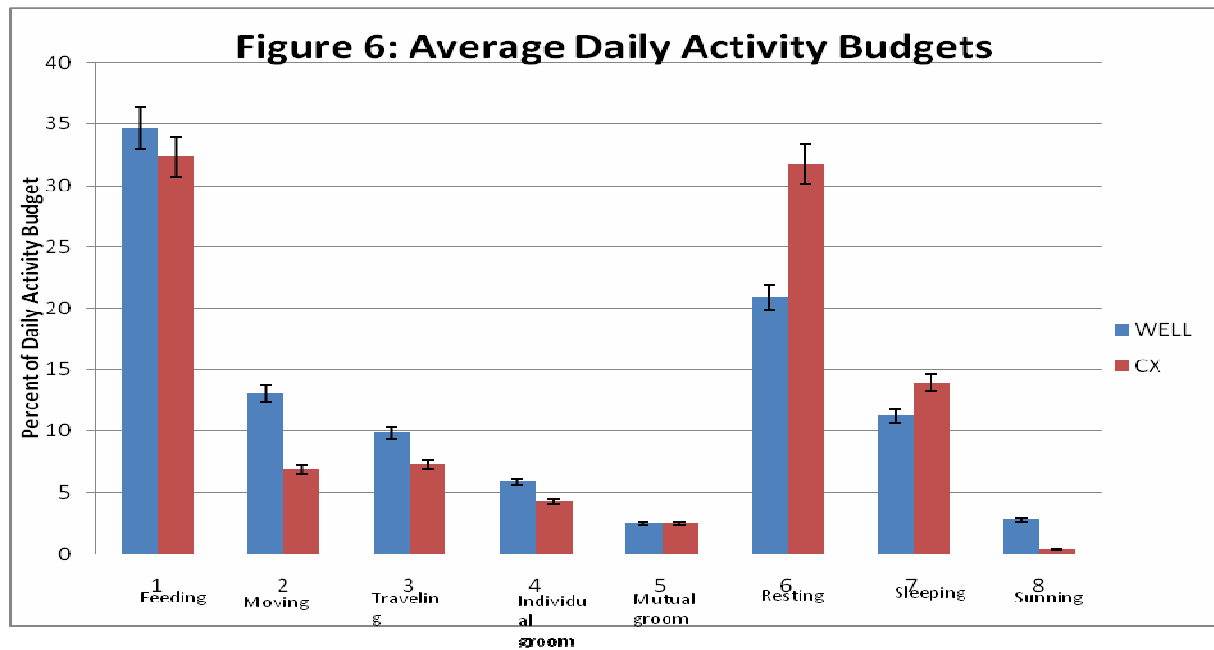
although this was not proven in the transect evaluation. (Razafindramanana, unpublished data)



## Activity Budget

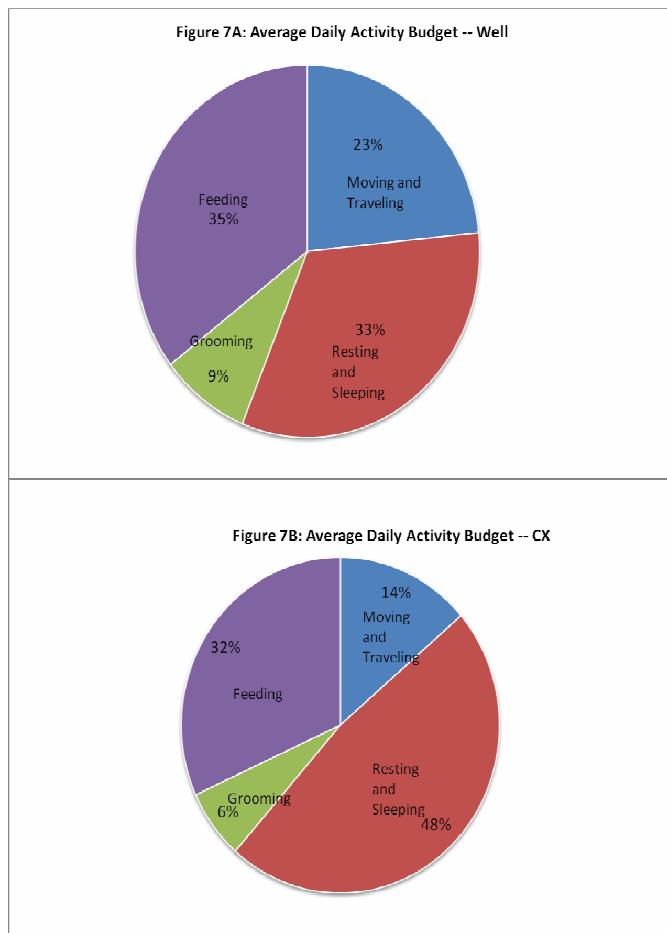
Results concerning daily activity budget show considerable variation between the two troops, especially in time spent resting as well as moving/traveling. Figure 6 below compares the average daily activity

budgets of the two troops by comparing the percent of time each troop engaged in each of the eight observed behaviors.



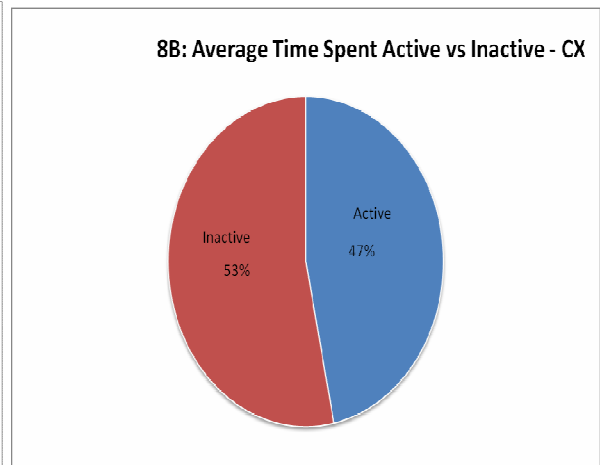
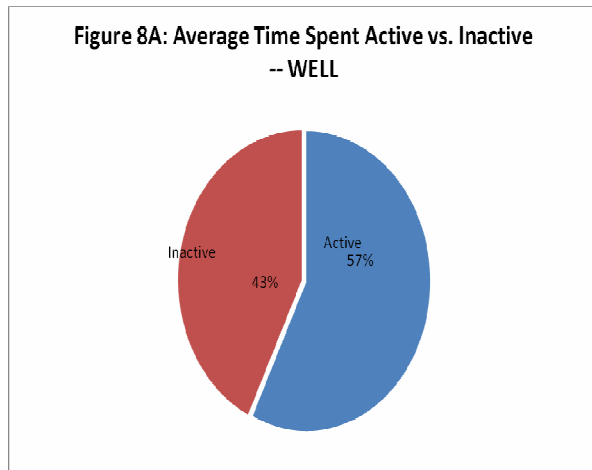
CX was observed to spend a significantly greater percentage of time resting than WELL. ( $p \leq 0.05$ ) This inactivity corresponds to a significantly lower percentage of time spent moving ( $p \leq 0.05$ ) WELL spent a greater percentage of time traveling but although this difference is noticeable it did not prove statistically significant. However, due to a greater surface area covered per day ( an average of 13437.375 square meters per day versus 4453.125 square meters per day), it can be inferred that WELL traveled greater distances per day, despite the fact that they did not spend significantly more time traveling.

The figures below represent the average proportion of daily activity allotted to the following categories: feeding, moving and traveling, resting and sleeping, and all grooming activities. Amount of time spent sunning is not included because of the insignificance of time allocated to this activity.

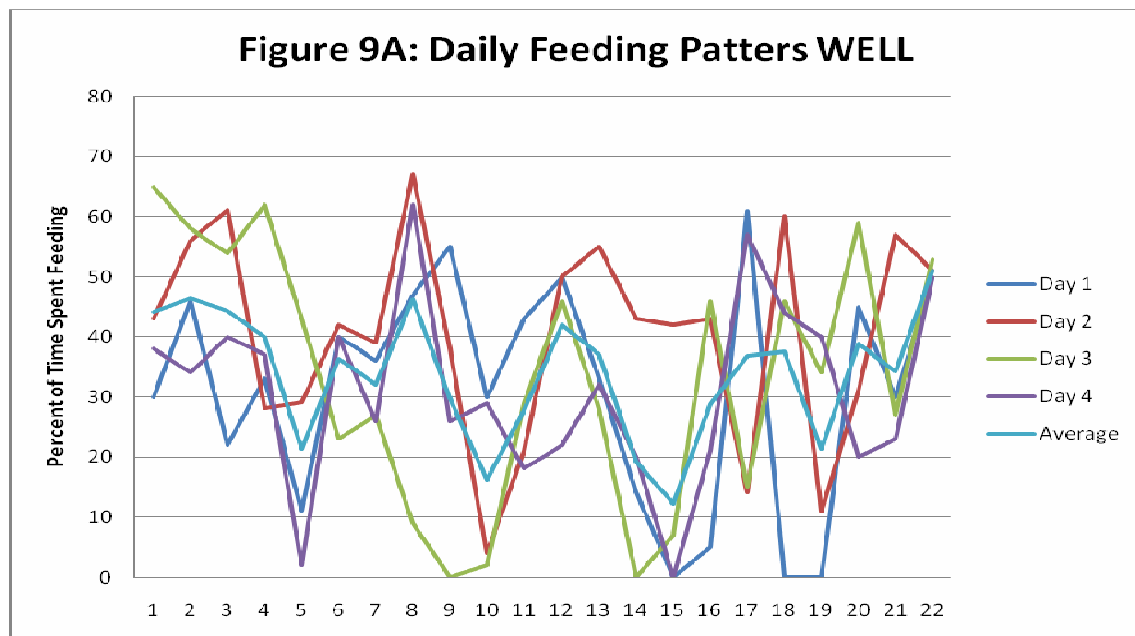


Significant differences in daily activity budget are revealed in these figures: CX spent an average of 48 percent of the day resting and sleeping whereas WELL spent an average of 33 percent of their time engaging in these activities. Moving and traveling are grouped together for comprehensive analysis and reveal a significant discrepancy ( $p \leq .002$ ), which is more statistically significant than either moving or traveling alone.

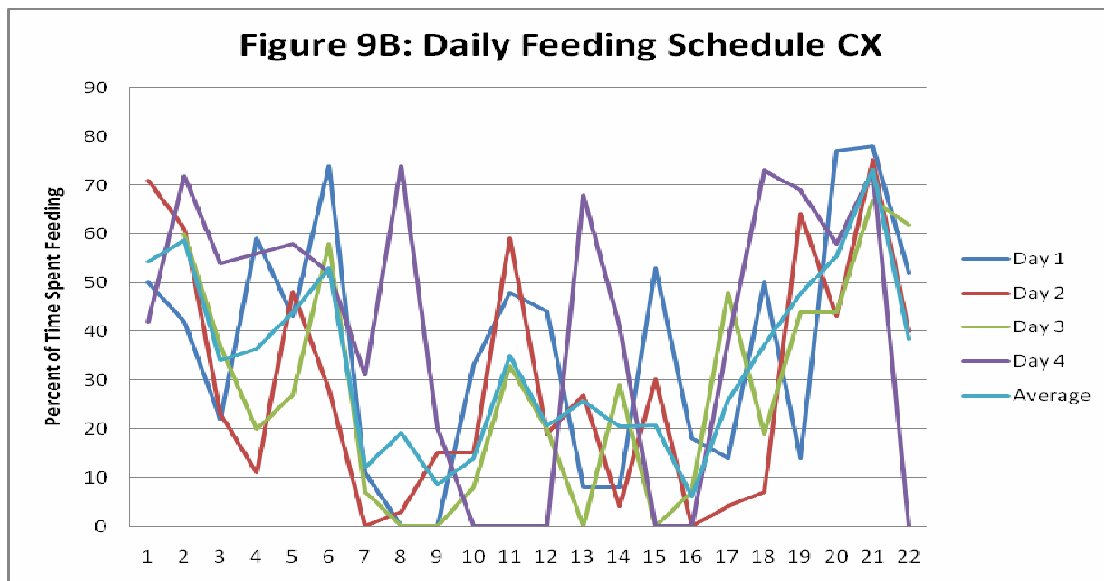
The proportion of time spent engaging in active versus inactive behaviors reinforces the above conclusions. WELL was active for a greater percentage of time than CX, though this did not demonstrate statistical significance.



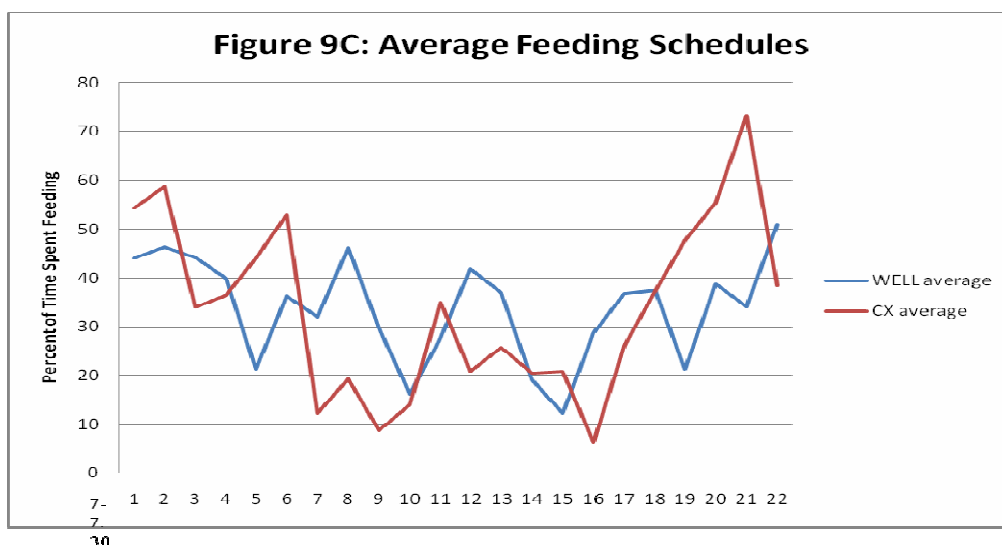
Although percent daily time allotment to feeding was not notably different between troops, (slightly greater for WELL than for CX) daily feeding patterns shown below in figure 8 reveal interesting differences in feeding behavior throughout the day. The x-axis corresponds to half hour intervals beginning with 7h00.





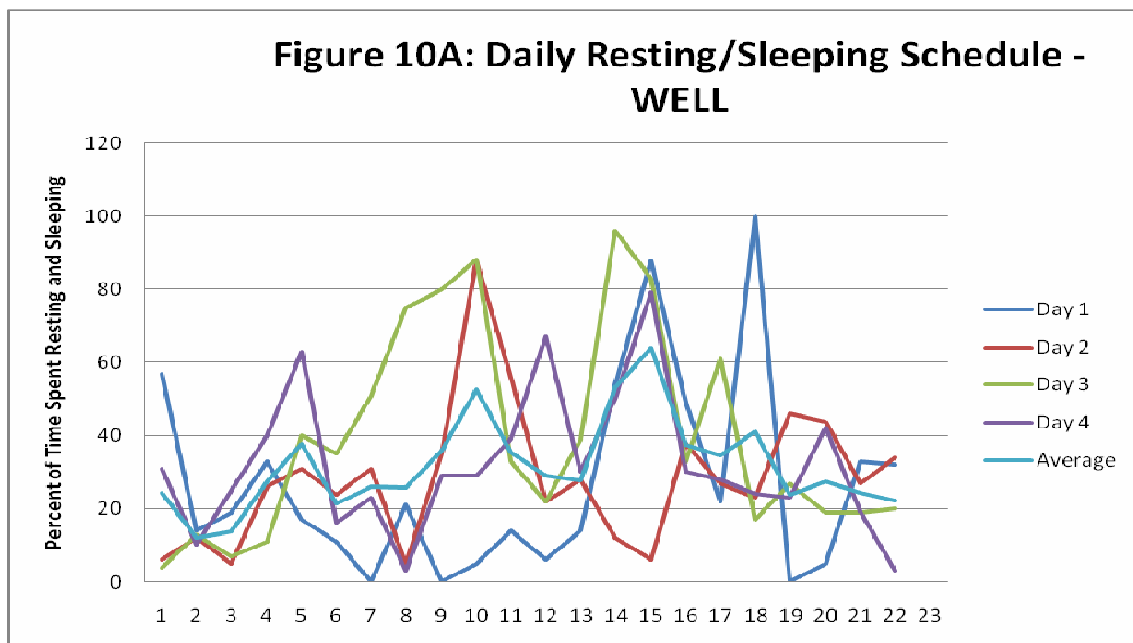


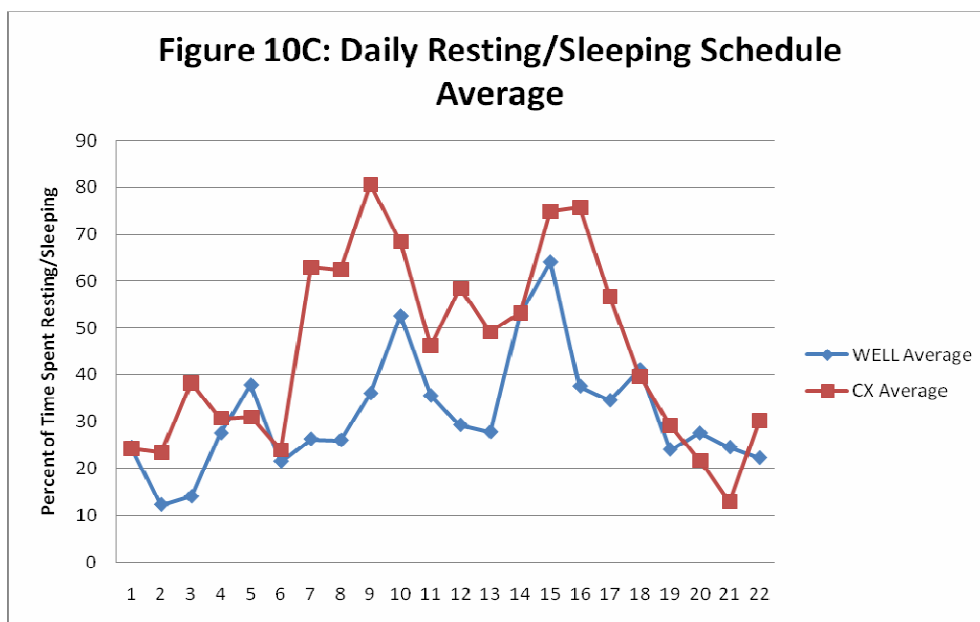
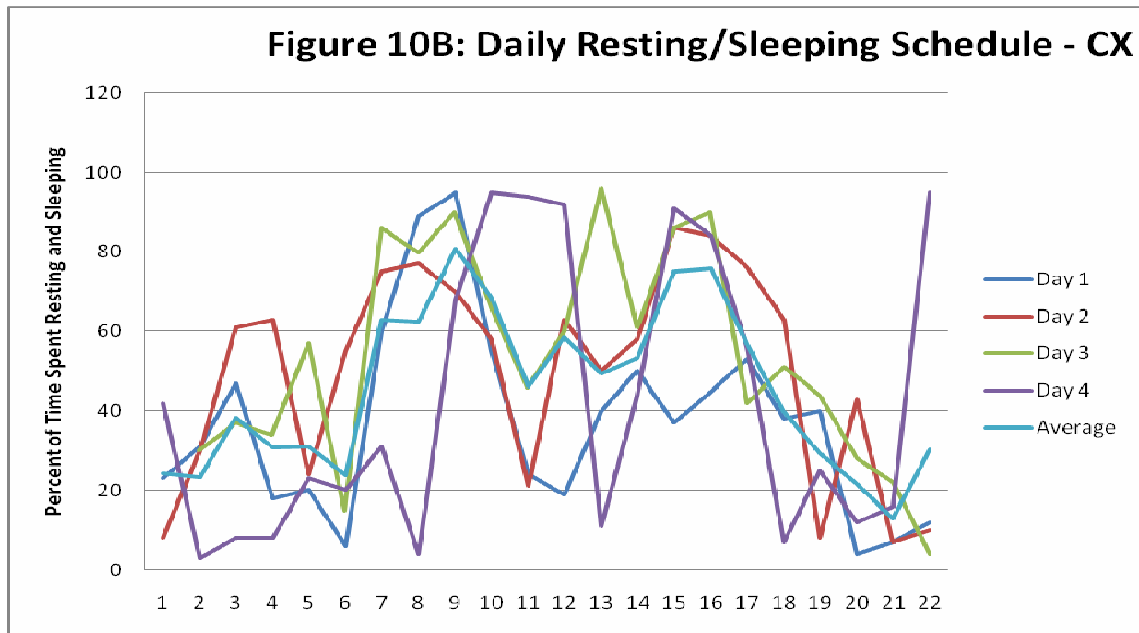
The time interval with the most significant discrepancy between groups is 5-5.30 when CX experienced an intense bout of feeding (almost 80 percent feeding.) Differences in feeding schedule for the two groups can be more easily deduced by examining only the study averages, as seen below in figure 9c.



In general, periods of heightened feeding are in the morning and evening, with the middle of the day reserved for more inactive activities. Both

groups interrupt resting time in order to feed in the middle of the day, though WELL experiences a shorter, more intense feeding period midday while CX's midday feeding is more prolonged. In addition, CX and WELL seem to experience opposite feeding patterns from 8h30 to 11h00. A greater percentage of WELL individuals feed during the second half of this time period, whereas a greater percentage of CX individuals feed during the first half of this time period.





Sleeping and resting time is higher in the middle of the day as opposed to early and late for both troops, but peak resting times occur on two different occasions around 11-11.30 and 2-2.30 with a period of activity in between. Feeding is relatively high during this time period (see figure 9) this break from

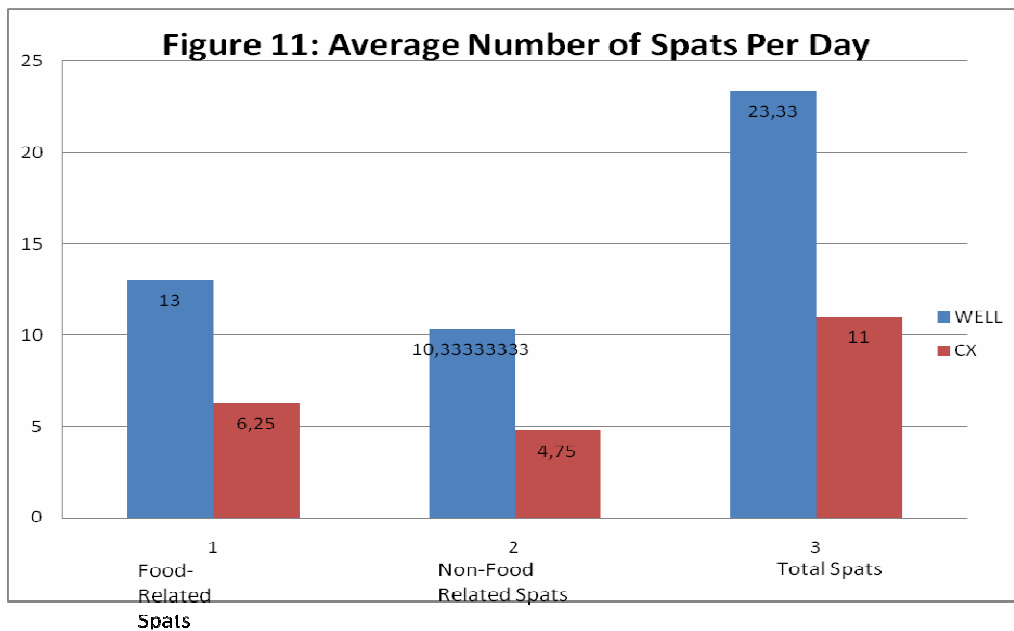
resting and sleeping mid-day to feed is more pronounced in the WELL group (figure 9A.) Although the activity pattern is similar between the two groups, CX exceeds the percentage of time spent resting of WELL troop at almost every time interval. Although each group exhibits variance in resting schedules among the four days of observation, there is not a remarkable difference between the two troops in respect to this variance.

### **Ad Libitum Social Behaviors**

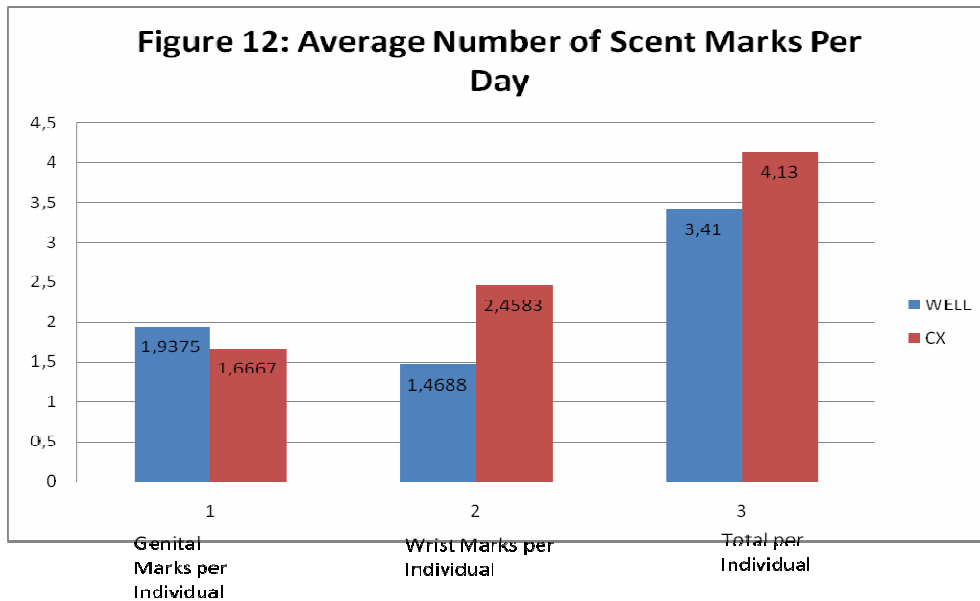
If data from the first day of observations is not included in the analysis of spats (I did not acquire accurate data due to difficulty identifying spats) then there is a significant difference in food-related spats between WELL and CX troops. ( $p \leq .005$ ) The standard deviation was twice as high for the data of WELL than CX when the first day is included in calculations. Therefore, when this outlying data set is excluded, there were significantly more food-related spats amongst the WELL group in Ankoba (average of 13 per day) as opposed to 6.25 spats per day in CX. If included, the comparison holds true but is not statistically significant.

However, the difference in food-related spats is no longer statistically significant when comparing food-related spats per feeding scan. Nonetheless, WELL troop had an average of .045 spats per feeding scan whereas CX had an average of .032 spats per feeding scan. WELL group may have more total spats because of its greater number of individuals: eight versus six individuals in CX. The calculation spats/ number of food scans

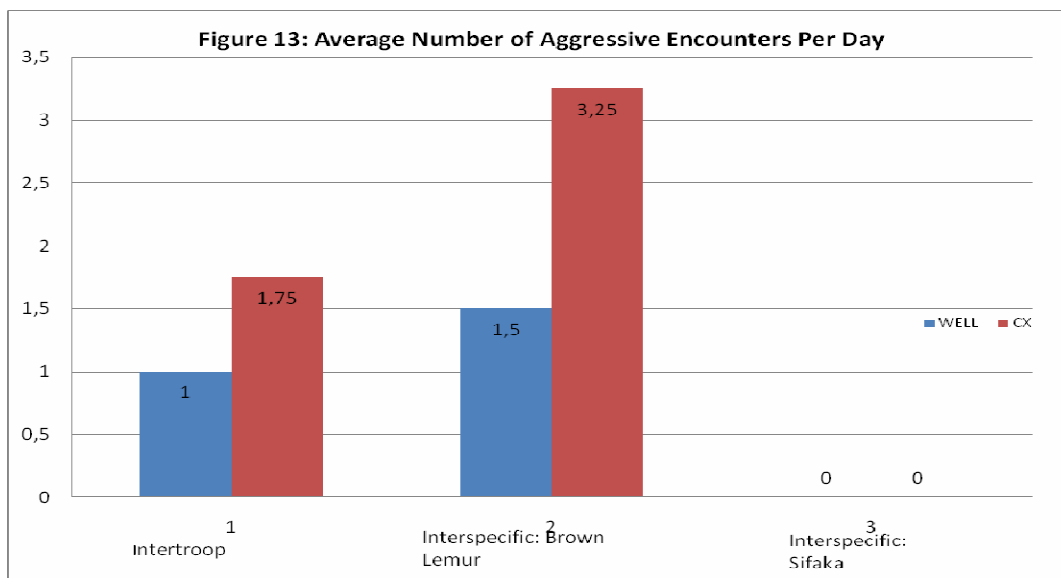
accounts for this population difference. In addition, there was no significant difference in number of food-related spats per feeding hour. (.16 for WELL versus .12 for CX) Well troop was observed to have a greater number of non-food related spats but unlike food-related spats it was not statistically significant. To account for differences in population size, I also calculated the average number of non- food-related spats per individual for each troop. WELL had an average of 1.29 non- food-related spats per individual per day whereas CX had an average of .79 spats per individual per day.



CX displayed a slightly greater average number of scent marks per individual, with .72 more scent marks per individual per day, as depicted in figure 12. This difference, however, is not statistically significant.



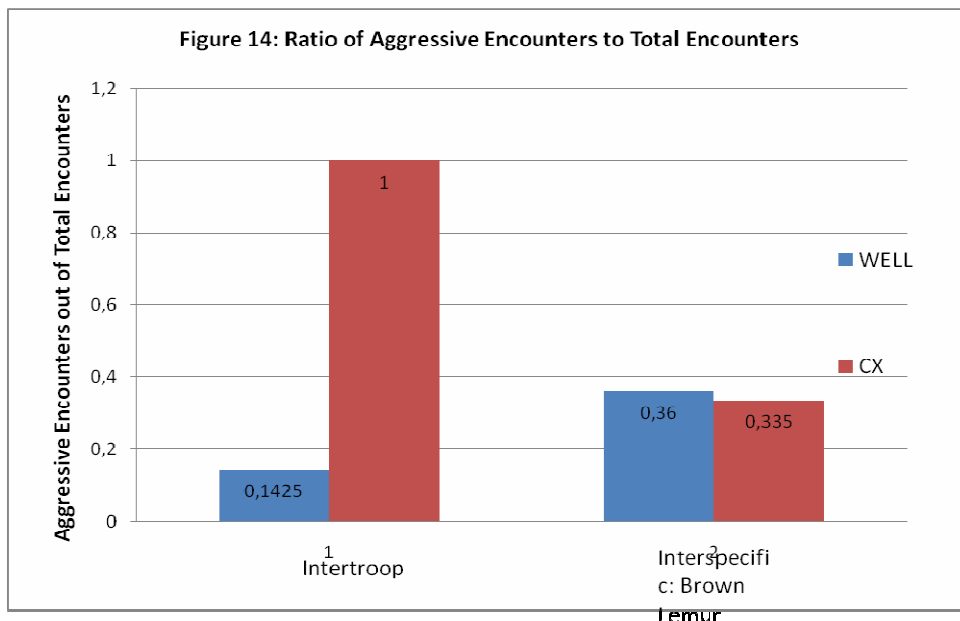
Whereas the WELL troop experienced greater intra-troop conflict (as seen in greater number of spats), CX experienced higher levels of inter-troop and interspecies aggression, as seen in figure 13 below.



When considering average number of encounters per day, CX troop experienced 1.75 times the frequency of inter-troop aggressive encounters and over twice the frequency of interspecific aggressive encounters with Brown Lemurs, (*Eulemur fulvus*). However, this difference proved to be

statistically insignificant. WELL troop had encounters with Sifaka, (*Propithecus verreauxi*) 13 times as often as CX, and this difference proves statistically significant. However, the encounters were all peaceful. Therefore, for examining the ratio of aggressive interspecies encounters to total interspecies encounters, statistics for encounters with Brown Lemurs were used exclusively.

In addition to a higher total average of aggressive encounters, CX also had a higher proportion of aggressive inter-troop encounters out of total inter-troop encounters, as shown in Figure 13. This disparity proved to highly significant ( $p \leq .005$ .) Encounters with other troops of *L. Catta* resulted in aggression 100 percent of the time for CX troop as opposed to 14.25 percent of the time for WELL. In contrast, the ratio of aggressive inter-species encounters to total inter-species encounters was similar between both troops. Therefore, CX has a greater frequency of aggression with Brown Lemurs, but this was correlated to a greater frequency of encounter.



## DISCUSSION

Disparities in behavior between the two troops can be explained through considerations of ecological characteristics of their differing habitats. Because the two habitats are in close-proximity to one another in the same reserve, variables such as mega-fauna constitution, climate, geographic location, and predation risk are not relevant. Vegetative composition is therefore the fundamental difference between the two habitats. Also, the functional and delicate ecosystem balances of natural, primary forests are not easily replicated in re-grown forest habitats.

The feeding ecology of *L. catta* is finely tuned to the seasonal nature of specific food resources. (Sauther, 1998) At Beza Mahafaly Reserve it was shown that early lactation coincides with an initial peak in fruit availability and a greater availability of new leaves occurs during the lactation/ weaning period. Lemurs have evolved to adapt to the extreme variable conditions of their environments by optimizing their intake of high-quality food during the rich, wet season. This coincides with the time of lactation and weaning and is an especially energy-costly time for female *L. catta*. (Wright, 1999; Ganzhorn, 2002). Therefore, ecological conditions can have significant effects on physiological processes and consequently social behavior. (Sauther, 1998) Species composition, phenology, and food availability are therefore essential to consider when examining the effects of habitat on *L. catta* behavior.

Though Ankoba may offer a greater total availability of food sources, Malaza contains a higher density and greater food availability of preferred



food sources essential to *L. catta* diet. CX's territory is of particularly high abundance of two preferred food sources: *Tamarindus indica* and *Rinorea greveana*. A study surveying six different gallery territories concluded that CX had the highest number of *T. indica* trees per troop member. (Koyama et al. 2006) Transects chosen in this study did not support this finding and therefore may not have been representative of the habitat. Measures of food availability were therefore affected. Though *T. indica* was shown to have a greater density in Ankoba according to my transect evaluation, Malaza forest remains the area with the highest density of *T. indica*, particularly the range of CX troop. (Koyama, et. Al., 2006; Soma 2006) This leguminous tree is the keystone food source of *L. catta* and the dominant species of the gallery forests inhabited by *L. catta*. (Budnitz and Dainus 1975; Rasamimanana and Rafidinarivo; Merti-Millhollen,2003) *T. indicus* produces fruit and young leaves asynchronously, thereby providing food resources for *L. catta* year round. (Sauther, 1998) At the time of study, it was observed that *T. indica* was the plant species in both habitats with the highest proportion of new leaves and leaf buds. Young leaves contain more water and nitrogen, and fewer toxins and digestion reducers than mature leaves and are therefore selectively exploited. (Simmen and Sabatier, 1996) CX used the key tree species as its food source 36 percent of the time, whereas WELL exploited it only 28 percent of the time. Therefore, CX consumed a diet richer with leaf buds, in fact twice the amount: 30 percent versus 14 percent for WELL. WELL consumed a greater proportion of less nutritious mature leaves.

Despite higher densities of *T. indica* trees in Malaza, studies have revealed little regeneration of this species in a study area encompassing the range of CX. Over 11 years from 1989 to 2000, the density of *T. indica* trees has decreased from 12.7 per hectare to 11.2 per hectare. And because *L. catta* populations have increased in this time period, there are now less *T. indica* trees per individual. (Koyama, 2006) Ankoba showed signs of greater forest regeneration because of a greater density of small trees and saplings. Nevertheless, Ankoba supports a lower density of the key food source.

Fruit is a preferred food source for *Lemur catta*, and troops feed on it whenever it is available. (Merti-Millhollen, 2003) Fruits are valuable for their high concentrations of soluble sugars and low fiber content. (JCambell et al., 2004; JLambert, 1998) The time of this study coincides with peak *Rinorea greveana* consumption (November and December.) (Soma, 2006; Pride et al, 2006) *R. greveana* fruit has been identified as a high energy and high quality food source (Pride et al, 2006; Rasamimanana, 2006) Malaza forest had both a greater density of this tree species and greater green fruit available per tree. CX fed from *R. greveana* 42 percent of the time and their diet correspondingly comprised 43 percent green fruit. In comparison, WELL troop exploited *R. greveana* only 31 percent of the time and their diet consisted of 28 percent green fruit. WELL troop supplemented their diet with the ripe fruit of the introduced species that dominates Ankoba, This species may not be as rich and productive a food source as *T. indica* and *R. greveana*. It contained ripe fruits at the time of the study that comprised 22 percent of WELL troop's

diet. The species contributes to greater total food availability in Ankoba, but Malaza has greater food availability of higher quality food sources preferred by *L. catta*.

In this study, Malaza was found to have greater levels of species richness. Despite the addition of introduced species in Ankoba, the transect chosen in that habitat contained five unique tree species as opposed to seven in Malaza. However, Rambeloarivony found in his dissertation study that both forests have nine native trees and Ankoba has an additional three introduced species. Overall species richness, however, is not an accurate indication of the health of an environment. Abundance of native food sources may be more important. Rambeloarivony found that only 33.82 percent of trees in Ankoba are native whereas Malaza is a hundred percent native.

It is important to note that though there are no introduced species in CX's home range, the troop makes excursions during the dry season to feed on introduced plant species grown in the tourist front. (Soma, 2006) In fact, during the late dry season, CX was observed outside its territory 89.2 percent of the time as opposed to the wet season when it remained in its territory 88 percent of the time to feed on endemic species. In the early wet season (also the time of my study) CX did not feed on introduced species, concentrating instead on endemic species such as *R. greveana*. *L. catta* utilize these introduced species, such as *A. indica*, *C. sinensis*, and *L. leucocephala*, during the dry season when endemic food sources are less

available. *L. catta* exhibit plasticity in feeding behavior: switching to new food sources based on seasonal availability. These introduced species can be beneficial food sources because they offer availability of top-ranking plant parts during harsh seasons, can grow in easily defensible patches, and perhaps have high nutritional content. Introduced species can also be potentially dangerous. *L. leucocephala* leaves are more nutritious and energetic than those of *T. indica*. However, the species has been shown to cause alopecia in lemur populations at Berenty. (Soma, 2006) Nevertheless, introduced species may act as buffers for severe seasonal climate variation and may lead to increases in population density. Research investigating the effects introduced species have on lemur populations is of particular conservation interest.

Though few studies have examined nutritional benefits or possible disadvantageous to consumption of *P. dulce*, the leguminous tree is reported to have protein rich flowers and fruits. (Blumenfeld-Jones et. al., 2006) However, I argue in this paper that the species is an inferior food source compared to native species found in Malaza (especially *T. indica* and *R. greveana*.) Despite consuming this additional introduced food source, the lemur troop inhabiting Ankoba displayed behaviors indicating lower-food availability than the troop in Malaza.

Greater availability of ideal food sources in its habitat allows CX to spend less time moving and traveling in search of these resources. This translates into a smaller territory size and greater allotment of time to resting.

Territory size is shown to be inversely proportional to food abundance. (Anderson, 2008; Blumenfeld-Jones et. al., 2006) With decreasing food density, home ranges must increase to meet demands of minimum food intake. This suggests that CX occupies a home range smaller than WELL because the troop is able to meet its energy demands without needing to expend extra energy traveling. The territory of CX was three times smaller than that of WELL. Accordingly, CX spent less time per day moving and traveling, and more time resting. The territory of both CX and WELL were smaller than average territory sizes for *L. catta*, which are typically six to twenty-three hectares. Previous studies of CX have reported territories larger than the range found in this study. (Soma, 2006) This may be a result of the short length of the study: the troops may have not visited all of their range in the four days I followed them. Alison Jolly found that *L. catta* will cover 80 percent of their home range in ten days in one season. (Jolly, unpublished data; Mertyl-Millhollen, 2003)

Differences in percentage of time spent feeding were minimal but because moving was defined as movement within one tree, the fact that WELL spent a considerably greater amount of time moving may have been in search of quality food products. CX, in contrast, with an abundance of key resources was able to spend extra time resting. There was no significant difference in either patches exploited per day or patches exploited per feeding time. This may be due to the short period of observations. According to optimal foraging strategy, troops in food-rich territories should exploit a greater number of patches per day. (Saucier, 2008) Because of high-food

density, the energy benefit from exploiting a new patch outweighs the costs of traveling to the patch. For troops in food-poor habitats, movement among patches is more energetically costly. Thus the strategy is to spend more time feeding per patch to save energy.

The high proportion of CX's daily activity budget devoted to resting and sleeping may be partially explained by the effects of abnormal temperatures during three out of four days data was collected. Day two and three of observation had midday temperatures of approximately 40 degrees Celsius. Day four of observation was cold and windy with a midday temperature of 22 degrees Celsius. Unfortunately, temperature was not recorded for the days of observation of WELL, but they can be assumed to be around 30 degrees Celsius. The possible effect of this abiotic factor is supported by the standard deviation in time resting for CX which was twice as high as that of WELL. On the first day of observations of CX, the temperature did not differ markedly from the temperature of the days spent with WELL. On this day, the troop spent 29.3 percent of time resting, 6.1 percent sleeping), and 18 percent moving and traveling. The average for all four days of WELL observation was 20.9 percent resting, 11.2 percent sleeping, and 22.8 percent moving and traveling. Therefore, the conclusions made thus far hold relevant even if only the first day of CX observations are regarded: CX spent a greater amount of time resting and a lesser amount moving and traveling. The effects of temperature may have merely exaggerated this trend.

Differences in incidence of aggression can also be explained as an effect of food-availability in the two habitats. Between-group feeding competition is shaped by total food abundance, while inter-troop competition is strongly affected by food distribution within a home-range. (Elwanger, 2002) The WELL troop experienced greater intra-troop conflict (as seen in greater number of spats), whereas CX experienced higher levels of inter-troop and inter-species aggression. Since a majority of these antagonistic interactions occur over food resources, it may be concluded, then, that WELL experiences more intra-troop competition while CX experiences greater levels of inter-troop and inter-species competition. If Intra-troop competition occurs as a result of food scarcity within a troop's territory, then greater intra-troop competition in Ankoba reflects lower food availability. In contrast, studies have shown inter-troop competition to be elevated in food rich areas, as troops compete for the choicest resources. (Goodman,2006). In 1997, neighboring troops frequently invaded the center of Troop CX's range because of the presence of an artificial water cistern and several large *T. indica* trees. (Takahata, 2005) Pride 2005 argues that groups living in high quality ranges are more likely to experience inter-group encounters than those in ecologically scarce ranges, most likely due to greater population densities. (Pride 2005; Jolly 2002) Population varies based on rainfall, food availability, and habitat type and *L. catta* densities can range from 600 individuals per square kilometer in areas with introduced fruit trees and constant supply of water to 250 individuals per square kilometer in

naturally occurring gallery forest. (Goodman, 2006) In addition, greater levels of inter-troop competition in CX troop may be explained by the size of its home range. Due to social changes such as troop divisions and evictions, the number of troops in Koyama's study area (including the range of CX) increased and territory size decreased during his 11 year study. CX shows signs of increased aggression in order to defend its smaller territory. (Koyama, 2006)

This disparity in frequencies of aggressive encounters may be explained, at least partially, by differences in group size. Larger groups experience heightened levels of intra-troop competition whereas smaller groups are more vulnerable to inter-troop competition. (Pride, 2005) Some behavioral costs, such as foraging effort, day range, and agonism may increase with group size (Pride, 2005) As group size increases, more individuals will be sharing a given food supply which leads to exploitation competition. In addition, interactions among rivals may prevent group members from exploiting the food source efficiently, (or interference competition) in this case resulting in increased levels of food-related spats.

In contrast, other behavioral costs decrease with group size, such as predator detection, territory and food patch defense. (Pride, 2005) WELL may have lower levels of inter-troop aggression because of their greater size. CX may have had a slightly higher frequency of scent marking per individual because of their heightened need to defend their home range on account of their small size. CX's territory was determined to cover a smaller area, which increases their need to maintain it, hence a greater observed frequency of



scent marking. Animals in small groups have fewer partners to defend territory or food patches against competitor groups of greater size. If food patch quality is variable and patches are defensible, inter-troop food competition may favor larger groups that can monopolize valuable resources. (Pride, 2005) However, eight individuals is still well under average troop size for *L. catta*. WELL is therefore considered a small group and probably more closely resembles CX in terms of costs of group size. A better explanation is CX's need to assert its territory in its food-rich habitat. CX also experienced more inter-troop confrontations, which increases the need to assert territory by scent marking.

Both troops experienced little aggression with *P. v. verreauxi*. This inter-species coexistence is a result of little dietary overlap between the two species: *P. v. verreauxi* exhibit by far the greatest level of dietary diversity among the three lemur species found in Berenty. (Simmen, 2003) However, aggression with *Eulemur fulvus rufus* is an important aspect to consider. The species was inadvertently introduced in 1975 and now sustains populations reaching densities comparable to those of the ring-tailed lemurs. (Simmen, 2003) The two species share a substantial number of dietary food sources but partition their resources: *L. catta*'s terrestrial habits allow them to consume species not accessible to canopy-dwelling *E. fulvus*. However, in the study of Simmen et al. 2003 investigating dietary overlap between the two species, a total of 18 plant species were shared between *Lemur catta* and *Eulemur fulvus*. Dietary overlap was found to be 79 percent during the wet season

owing to consumption of whole immature pods and mature leaves of *Tamarindus indica* by both species. (Simmen, 2003) *E. fulvus* often displace *L. catta* from food resources and are their main competitors. (Goodman, 2006)

CX experienced greater frequency of aggressive encounters with *E. fulvus* than WELL which may reveal greater competition over resources in Malaza forest than Ankoba between the two species, although this difference was not statistically significant. The ratio of aggressive encounters to total encounters was similar between the two troops, revealing that CX did not react more aggressively than WELL during encounters with *E. fulvus* but that the frequency of these encounters was higher. Malaza forest may be able to support higher densities of the two species which results in greater levels of interspecies competition.

Although this study resulted in statistically significant results, there are limitations to consider. Due to the short length of study, data may not be fully representative but nevertheless shows basic information for further research and conservation planning. The small size of troops selected results in a smaller sample size which can affect results. The level of aggressive encounters was not measured, which may affect results of intra-troop, inter-troop, and inter-species encounters. Finally, the transect taken (160 square meters) may not have been large enough to fully represent the home range of the troop.

## **CONCLUSIONS**

Although *L. catta* is an ecologically flexible species that can survive in a variety of ecosystems in southern Madagascar, it is nevertheless finely tuned to the harsh seasonal variation and phenology of its habitat. (Elwanger, 2002) In particular, the loss of gallery forests would greatly impact the numbers of surviving lemurs in Madagascar (Sussman et. al., 2003) *L. catta* at Berenty profit from habitats relatively free of anthropogenic threats, and their densities have increased dramatically since Alison Jolly began her studies there in the 1960's. (Takahata, 2005) This study reveals the behavioral disparities between troops living in natural versus old-second-growth replanted forest. Divergences in feeding behavior, activity budget, and antagonistic encounters are a result of the differences in species composition and food availability in their two distinct habitats, especially as a result of the introduction of non-native species in the re-grown habitat. These differences are statistically significant and reveal the nonreplicable advantageous of old-growth primary forest natural habitat.

*Leucaena leucocephala* was introduced to Berenty in the 1970's at a time when the species was being largely promoted in tropical areas for reforestation and source of food for livestock. The species thrives in disturbed areas with low levels of seasonal rainfall, making it an ideal species to plant at Berenty. (Hansen, 2006) Its dangerous effects on lemur populations was later discovered—it contains mimosine, a toxic compound that causes alopecia, weight loss, thyroid dysfunction, and ill thrift in animals. *L. leucocephala* is a case study example of the dangers of introduced species.

Introduced species can, however, benefit lemur populations consuming their food resources. They can provide a nutritious source of food during periods of low food availability of native species. Introduced fruit trees are proposed for reforestation because of their ability to provide food to buffer the effects of food scarcity, especially in the dry season, which can lead to population growth (Soma 2004, 2006) However, *L. catta* are finely tuned to seasonal variation in native species and the effects of introduced species to this delicate balance is insufficiently studied. If *P. dulce* is a nutritious food source why does WELL exhibit characteristics of a troop in a more food-poor environment? This study would suggest *P. dulce* is not as productive a food source as native species such as *T. indica* or *R. greveana*. It may be preferential to plant native trees and maintain the natural forest composition to ensure species preservation. However, this is time-consuming and deforestation is rapid. To create corridors between patches of protected areas, it may be less important to preserve the native composition of the forest in favor of quicker solutions.

Most reforestation projects in Madagascar consist of exotic tree plantations of eucalyptus and pine grown to meet the increasing demands for charcoal and firewood production. (Gade and Perkins-Belgram, 1986) Native tree species typically are slow to regenerate after deforestation. In contrast, Eucalyptus is a fast-growing biofuel but also ecologically damaging (absorbing surrounding moisture and hindering native tree growth) and is not thought to support lemur populations. (Gade and Perkins-Belgram, 1986)

Nevertheless, a study conducted on Eucalyptus plantations bordering eastern rainforests showed use of old plantations by lemur species: providing food, resting, and traveling opportunities. (Ganzhorn, 1987) However, population densities are much lower in monoculture plantations and mixed-species plantations are reported to be a superior alternative for supporting primates.

As shown in my study, replicating the exact vegetative composition and food availability of natural forest in a re-grown habitat is difficult and may not be practical for biofuel production. The goal of re-grown forests should be to provide habitat corridors to extend habitat for lemurs, act as buffer zones, and possibly support limited wood harvesting. Since forest fragmentation and therefore reduced gene flow are major threats to lemur populations, reforestation should be an important tool for creating buffer zones to reduce forest fragmentation. (Ganzhorn et al. 1996/1997) Studies have been conducted over the past decades to evaluate the suitability of both native and introduced trees for plantations (including the study on *P. dulce* by Blumenfeld-Jones 2006) Unfortunately reforestation as a conservation and biofuel strategy has decreased in recent years. Ganzhorn et al. argues that because lemurs do quite well in plantations and biofuel is in short supply, reforestation, especially of native trees should be included in every development plan in Madagascar. (Ganzhorn et al. 1996, 1997) Remaining native forests will not be able to support the country's need for fuel and construction wood. Tree plantations are urgently needed not only on the high plateau but in villages surrounding forests. And they should not be comprised

solely of Eucalyptus or pines. There are native and exotic trees that can provide fuel, fruit, honey and timber, and habitat for lemur populations, (Blaser 1993; Ganzhorn 1987) thereby reducing pressure on native forests.

The privately owned re-grown forest at Berenty is a special case of reforestation efforts in Madagascar. It is an old-growth secondary forest that is highly effective in supporting lemur populations and is an important ecotourism site in the region. However, the forest was not grown to mirror the natural forest adjacent to it, but instead is dominated by an introduced species. Food availability of preferred food sources is lower in the habitat, forcing resident troops to maintain greater territories in order to find adequate food sources, changing the activity budget by increasing moving and traveling time and decreasing resting time, and increasing intra-troop competition. However, due to rapid rates of deforestation throughout the island, re-grown forests such as Ankoba should be considered adequate as habitat for lemurs and effective in providing ecological services, though careful attention to the use of introduced species should be paid.

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