Behavioral Disparities Between Two Troops Of Lemur Catta *That Occupy Different Habitats*

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ABSTRACT

The present study was conducted during the early wet season at Berenty Private Reserve. It investigates behavioral disparities between two troops of Lemur catta *that occupy different habitats—gallery forest and scrub. Methods included density and phenology analysis to evaluate relative food availability in each territory. Behavioral observations were collected across eleven full-day troop follows. Results show extensive, statistically significant differences between behavior in the gallery and the scrub, many of which can be explained by relative food abundance within a troop's home range. Some trends included greater intra-troop discord and fewer inter-troop conflicts in the scrub. In addition, the troops demonstrated significant disparities in time spent feeding per food patch; this result reflected optimal foraging strategies within habitats of different food densities. Finally, the inter-troop differences in daily activity budget and schedule were extensive. One general trend was reduced activity levels, including less time spent feeding, in the scrub. Overall, the present study seems to suggest that food abundance within a territory has considerable and multidimensional effects on* Lemur catta *behavior.*

INTRODUCTION

Ringtailed lemurs are the flagship species of Madagascar. They cling to cotton tee shirts with long, elegant fingers and stare out of postcards with impish eyes. These beautiful animals captivate and enchant thousands of tourists each year. Nevertheless, their charm is exceeded by their intrinsic value to science. Behavior cannot be fossilized like bone; thus, determining the course of its evolution relies on considerable inference and extrapolation. It is for this reason that the value of *Lemur catta* is particularly pronounced in the arena of behavioral biology. Ringtailed lemurs, as prosimians, are among the most primitive of all extant primate species and represent a crucial link in the evolutionary history of human beings. Allison Jolly, the leading expert in *Lemur catta* biology, remarked that this species "exemplify both the convergence between prosimian and anthropoid social systems and the differences between them" (Jolly et.al., 2002). As such, knowledge derived from the effects of environment on extant prosimian behavior can be applied in the context of evolution and provide indications of selective environmental pressures that may have acted upon the evolution of primate behavior. Accordingly, the present study was designed to evaluate the influences of habitat composition on the behavior of *Lemur catta*. Of particular interest were the effects of relative food abundance and variety on activity budget, feeding strategies, and social behaviors.

BACKGROUND

Lemur catta

Among all prosimians, *Lemur catta* has been the species most extensively studied (Jolly, 2004). Ringtails are diurnal primates that have been described as both terrestrial and arboreal. They are social animals that live in multi-male, multi-female troops numbering roughly six to twenty-four individuals (Anderson, 2008). Territories are well-defined and fiercely protected. Although rigid intra-troop hierarchies dictate social interactions between members of each gender, males are unwaveringly subordinate to females.

In the wild, *Lemur catta* exist exclusively on the island of Madagascar. They are an IUCN Red-Listed, vulnerable species with a population that has plummeted as their habitats have been degraded and, in some regions, completely decimated by human activity (Ganzhorn, 2008). The majority of their natural range, stretching across Southern and Southwestern Madagscar, is dominated by spiny brush. However, the distribution also extends into corridors of dry deciduous forest in the Western lowlands and a few montane habitats in the central highlands. (Goodman et.al., 2006).

Lemur catta Diet

In general, Ringtail feeding behavior is largely "unselective and opportunistic" (Simmen et.al., 2006). In some regions, *Lemur catta* has been observed exploiting upwards of one hundred plant species. They consume fruits (both ripe and unripe), leaves (both young and mature), stems, flowers, seeds, dirt, and decaying organic matter. Occasional dietary supplements include invertebrates and, more rarely, small vertebrates as well. Despite the breadth of food sources consumed annually, only a few species contribute significantly to diet at during any one month. In fact, *Tamarindus indica* is the only food source exploited throughout the year in sizable quantities (Simmen et.al., 2006). As such, *T. indicas* is regarded as the keystone resource of *Lemur catta*. Ringtails feed on all parts of this tree and typically spend the night sleeping in its canopy (Blumfeld-Jones et.al., 2006).

Study Site: Berenty Private Reserve

Berenty Reserve lies along the Mandrare River in Southeastern Madagascar and has been privately maintained by the de Heaulme family since 1936. It is one of only four surviving patches of natural gallery forest along the Mandrare and one of only six protected areas populated by *Lemur catta* (Pinkus et.al., 2006). The main reserve at

Berenty encloses two-hundred hectares of scrub and gallery forest, and is inhabited by three species of diurnal lemurs—Sifakas (Propithecus verreauxi), hybrid brown lemurs (*Eulemur fulvus rufus x collaris*), and Ringtails. In addition to the river, the reserve is surrounded by open fields, a smaller reserve to the East, and a narrow, degraded corridor of spiny forest to the West (Jolly et.al., 2006; Jolly et.al., 2002). Berenty was opened to researchers in the early 1960s and has since been one of the foremost study sites in Madagascar (Jolly, 2004). Malaza, a ninety-seven hectare region at the center of the reserve, includes parcels of xeric scrub, open-canopy transition forest, and closed canopy gallery forest (Pinkus et.al., 2006). This was the site chosen to conduct the present study.

METHODS

The findings presented here reflect 260 hours of study, 150 and 50 of which were allotted for data collection and analysis respectively. The duration of on-site fieldwork spanned eighteen days in the early wet season, from November fourth to November twenty-first. Two days were dedicated to training and troop selection; in addition, one full day was required for an evaluation of food availability within both scrub and gallery habitats. The remaining fifteen days were reserved for collection of behavioral data.

Troop and Site Selection

In order to investigate any possible correlations between behavior and food availability within a home range, two troops from Berenty Reserve were selected to represent opposite extremes. One troop occupied a territory almost entirely within the closed-canopy gallery forest and the other was confined to a territory within the scrub. While the scrub presents a relative paucity of food that characterizes the vast majority of *Lemur catta* biogeography, the gallery forest is among the richest habitats populated by

Ringtails (Goodman et.al., 2006). Troop CX was selected as the gallery troop for the particularly high abundance of two preferred food sources within its territory. Koyama et al. (2006) surveyed six different gallery territories and concluded that the CX had the highest number of large *Tamarindus indica* trees per troop member. In fact, with 4.7 trees per individual, CX had nearly two and a half times as many as the territory with the second highest density of this critical food source (Koyama et.al., 2006). In addition, because annual peak in consumption of *Rinorea greveana* fruits coincides with the time of the present study, CX was also selected as the "rich" troop because it occupies the territory with the highest density of *R. greveana* within the gallery (Pride et.al., 2006). Figure 1A defines the CX territory and the distribution of *T. indicas* across the majority of the gallery forest (Koyama et.al., 2006). The density of *R. greveana* is illustrated by Figure 1B (Chapter 13).

FIGURE 1A

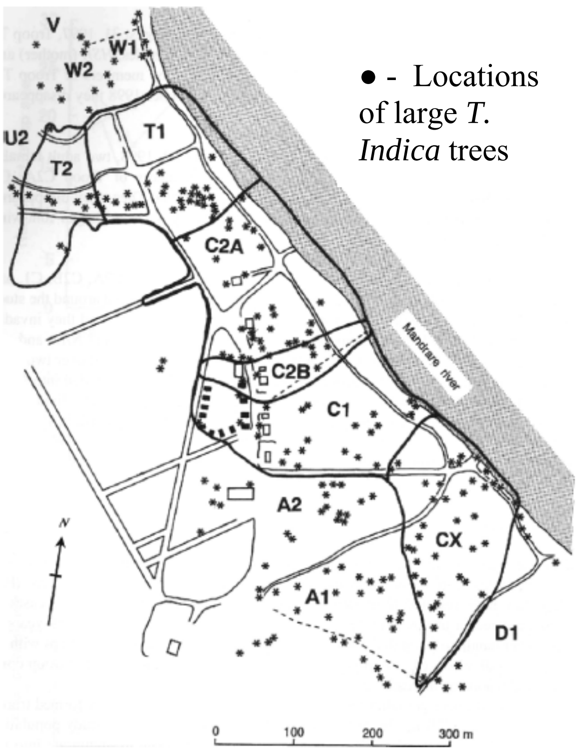
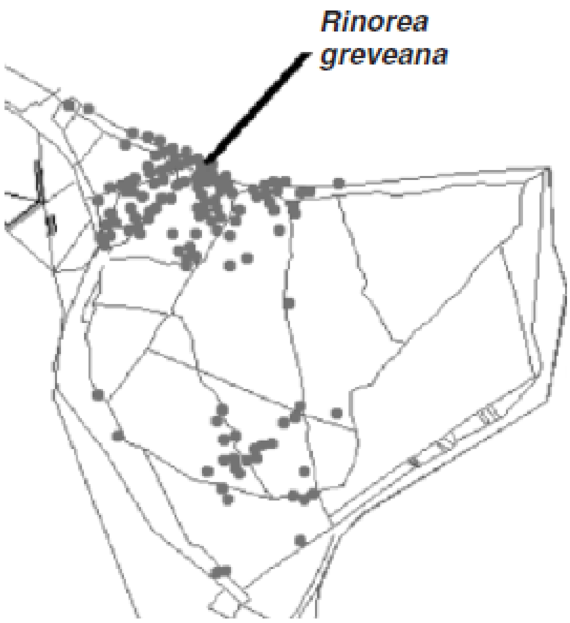


FIGURE 1B



CX is composed of nine individuals—six adult females, two adult males, and one infant. The scrub troop, also with nine animals—four adult males, three adult females, and one infant—was matched for group number but not composition. Therefore, small troops were deliberately chosen to facilitate comprehensive data collection.

Conducting the study at Berenty Reserve allowed for a comparative study of two troops from markedly different habitats but within close proximity to one another. Choosing a gallery troop and a scrub troop from two separate reserves would have introduced potentially confounding variables. Beza Mahafaly, for instance, is another gallery forest in Southern Madagascar and differs appreciably both in vegetation and lemur behavior (Pinkus et.al., 2006; Simmen et.al., 2006). Moreover, years of studies on *Lemur catta* at Berenty conferred additional benefits of the study site. The prior research provided detailed maps, extensive studies on vegetation, and valuable background information for troop selection. Additionally, due to the constant presence of researchers and tourists over the years, Berenty lemurs have become extremely habituated to people. This resulted in minimal observer effect on behavioral data.

Behavioral Observations

The behavioral data was compiled over eleven full-day troop follows, six follows of CX and five of Scrub Troop. At the launch of the study, the proposed design required six days with each troop that were to be scheduled in alternating series of three consecutive days. If the troop of interest was not located by 07h30, the follow was abandoned and reinitiated the next morning. This occurred on four separate occasions; three of which involved Scrub Troop. As a result, only five of the six anticipated Scrub Troop follows were able to be completed. In general, data collection began at 06h00 and ended at 18h00. However, bad weather prevented continuation past 16h00 on the third day of Scrub Troop follow. Also, once during a CX follow and once during a Scrub Troop follow, the troop was not located until 07h30, at which point data collection began and continued without interruption until 18h00. In total, CX and Scrub Troop were followed for 70.5 and 56.5 hours respectively.

Scan survey was the primary method for quantifying activity budget and feeding behavior. Every five minutes, the instantaneous behavior of each adult individual was recorded as Feeding, Moving, Traveling, Grooming, Mutual Grooming, Resting, and Sleeping. If the animal could not be located within thirty seconds, its behavior was not recorded. No distinction was made between feeding and foraging. Traveling was defined as movement, with tails raised, in one direction for at least ten meters across the ground; Moving was defined as any movement aside from Traveling, Grooming, and Feeding. Sleeping was defined as remaining stationary with eyes closed and resting was defined as remaining stationary with eyes open. It was also noted if resting or sleeping animals were huddled in direct contact with one another.

When an animal was observed to be feeding, the food source was recorded. If it was an unknown plant species, a leaf sample was taken for later identification by Josia Razafindramanana. In addition, tallies were kept to determine how many patches of each food source were exploited by the troop throughout the course of one day. Patches were defined as a single tree, bush, cactus, vine, decaying log, or invertebrate. A dirt or grass patch more loosely defined as a continuous area, no bigger than twenty square meters, that is at least seventy-five percent covered with the food source of interest.

In addition to employing the scan survey method, four social behaviors were noted ad libitum. First, each initiation of a separate mutual grooming session was recorded along with the number of individuals participating. Secondly, all spats were tallied and classified as either related to feeding (i.e. occurring during feeding time) or unrelated to feeding. Thirdly, all scent markings were recorded as either a male wrist mark, a male genital mark, or a female genital mark. Lastly, all forms of aggressive encounters were noted along with the level of the escalation and identity/gender the aggressor, the aggressed, and the winner. These encounters fell into three broad catagories: intra-troop, inter-troop, and inter-specific. For each conflict, the highest level of aggression was noted. These levels were quantified as follows: Level two- threatening movement in the direction of the other troop/individual; Level three- chasing; Level four- physical contact. Non-aggressive encounters with other troops—Ringtails, Brown Lemurs, or Sifakas—were recorded as level one.

Berenty Reserve is mapped into a grid with each quadrant measuring twenty-five by twenty-five meters. To facilitate calculations of home range area and distance traveled per day, a note of quadrant was added at each scan and each aggressive encounter.

Territory Evaluation

In order to estimate the availability of food within the scrub and gallery territories, two transects were taken. Each measured two meters by one hundred meters and was located within the heart of the troop's home range. The exact location of transects was chosen at random from a number of possibilities that had all been determined, through consultation of expert advice, to be representative of the vegetation density and variety as seen throughout the territory of interest.

Along each transect, the species, height, crown diameter, and DBH were enumerated for each tree exceeding ten centimeters in DBH. For trees with multiple trunks, DBH was recorded as a sum of all trunks that reached to or above breast height. The phenology study also included an evaluation of the availability of buds, leaves, fruits, and flowers. For each of these four plant parts, a tree received a score between one and four that was derived as follows from an estimation of the percent of the tree covered by the food source of interest: Score zero- zero percent, Score one- one to 25 percent coverage, Score two- 25 to 50 percent coverage, Score three- 50 to 75 percent coverage, Score four- 75 to 100 percent coverage. The score for fruits was split between ripe and unripe fruits, with each subcategory of fruit receiving a fraction of the total fruit score as determined by the relative abundance of each. Likewise, the score for leaves was divided between new leaves, mature leaves, and old leaves.

In addition to recording detailed phonologies for each large tree, transects were also surveyed for an estimation of canopy cover and number of small trees with DBH between five and ten centimeters. The percent of the ground covered by undergrowth—bushes, saplings, and vines—along with the coverage of grass was also noted. Again, these percentages were estimated on a scale from one to four, with each whole number increase corresponding to an additional twenty-five percent of coverage. These estimations were made every ten meters along the one hundred meter length of each transects.

Data Analysis

For analysis of scan survey data, the number of individuals engaging in each activity was added every thirty minutes, every hour, and as a daily total. These sums were then expressed as a percentage of total scan survey counts. (Note: one scan survey count refers to the observation of one animal during one scan). For instance, if four out of seven animals were observed for each of six scans between 08h00 and 08h30, the total scan survey count for those thirty minutes is twenty-four. Moreover, if a total of eighteen animals were feeding during those six scans, the percent feeding from 08h00 to 08h30 was recorded as seventy-five percent.

The more narrow categories of scan behaviors were also grouped together in two alternative ways for additional analysis. First, the behaviors were separated into Active and Non-Active behaviors. Active behaviors include grooming, moving, traveling, and feeding. Inactive behaviors include all sleeping and resting. Next, the behaviors were classified as Leisure, defined as grooming, resting, and sleeping, or Non-Leisure, defined as feeding, traveling, and moving. These four broader categories of behavior were analyzed holistically as a daily percent of total scan counts and by parts to determine the percent contributed by each component behavior.

Daily totals of activity budget, diet composition, distance traveled, and ad libitum behaviors were averaged for each troop. Daily averages were used in lieu of study totals due to the unequal time spent following each troop. Standard deviations and variance levels were determined. In addition, two-tailed T-Tests were employed to assess significance level.

Distance traveled was estimated by using the quadrant locations of each scan to superimpose the routes traveled onto a Berenty Reserve map. The length of each daily route was measured to the nearest centimeter and distance traveled was extrapolated through conversion of the scaled map units. Calculating the size of each home range relied on routes of travel and inter-troop encounters. First, locations of inter-troop conflicts that ended in victory or a draw were used to define clear territory boundaries. Then, a convex outline enclosing minimal area was traced along the quadrants surrounding the daily routes of travel. However, it is important to note that some outlying routes were deemed to be excursions and excluded from the home range.

For the evaluation of habitat and food availability, averages were calculated for ground and canopy coverage. Densities of small trees and of each species of large tree were also determined. In addition, average scores for availability of each food source—

leaves, buds, and fruits—were taken among trees providing that food source. For example, if ten trees were sampled and only two had fruit, one with a score of four and one with a score of two, then the average availability was recorded as (4+2)/2=3.

RESULTS

Home Range Determination

The home ranges for CX and Scrub Troop were found to cover 63,125 and 84,375 square meters respectively. Considering that *Lemur catta* is known to occupy territories encompassing between six and twenty-three hectares, these results are consistent with published reports of relatively small home ranges at Berenty (LemOfMad; Goodman et.al., 2006). The boundaries of each territory were established as presented below in Figures 2. Figure 3 (Blumfeld-Jones et.al., 2006) is provided as a reference to the placement of the home ranges in relation to different vegetation zones in Malaza.

FIGURE 2: Home Ranges

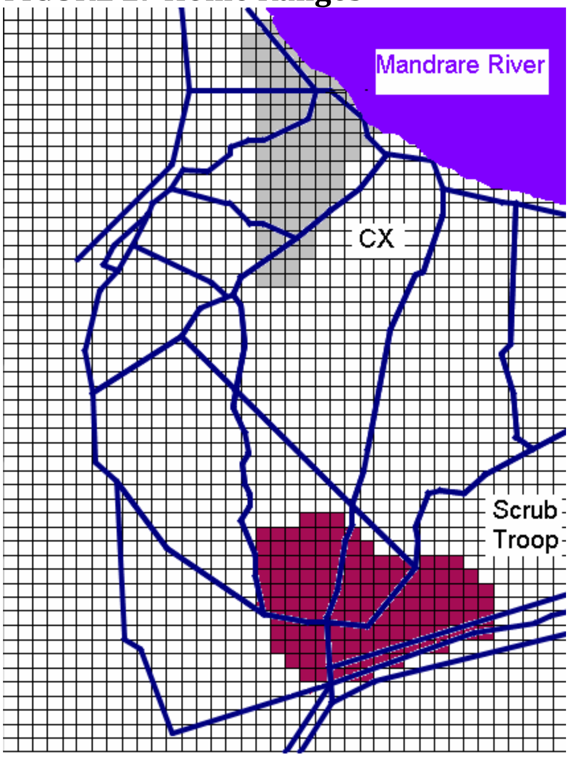
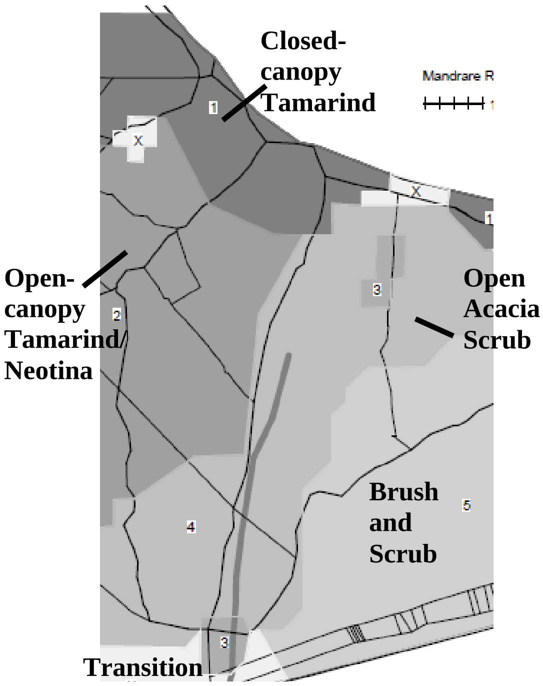


FIGURE 3: Vegetation Zones



Habitat Evaluation

The vegetation density and phenology evaluation revealed a sharp contrast between the habitats of CX and Scrub Troop. Below, Tables 1A and 1B enumerate averages and ranges in height, DBH, and crown diameter for each species of tree located within the transects and exceeding ten centimeters in DBH. Densities and average scores of food sources among each species are also provided.

TABLE 1A: Tree Abundance and Food Availability in the CX Range

Species	Density (Trees/ m^2)	DBH Average and Range (cm)	Height Average and Range (m)	Crown Diameter Average and Range (m)	Average Score for Leaves	Average Score for Fruits
Rinorea greveana	0,155	14,82 10-40	11,26 8-14	5,35 2-10	3,71	2,48
Neotina isoneura	0,015	30,00 26-38	21,67 20-25	10,00 8-12	4,00	0,00
Celtis bifida	0,015	23,83 11-415	17,00 13-25	6,00 2-11	1,67	0,00
Celtis philippensis	0,005	45,00	30,00	8,00	4,00	0,00
Terminalia sp.	0,005	31,00	25,00	11,00	4,00	0,00
Crateava excelsa	0,005	15,00	15,00	10,00	4,00	0,00
Tamarindus indica	0,015	68,33 12-100	16,67 12-100	24,00 5-25	4,00	1,33

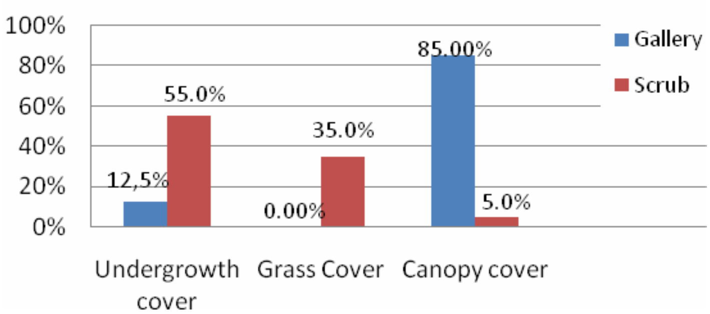
TABLE 1B: Tree Abundance and Food Availibility in the Scrub Troop Range

Species	Density (Trees/ m2)	DBH Average and Range (cm)	Height Average and Range (m)	Crown Diameter Average and Range (m)	Average Score For Leaves	Average Score for Fruits
Crateava excelsa	0,01	10,5 10-11	5,5 3-8	2,5 2-3	4	0,5
Opuntia vulgaris	0,005	10	3	2	n/a	0
Grewia salienta	0,03	13,58 10-21	9,33 4-12	3,67 2-5	2,17	0
Azima tetracantha	0,015	31,67 25-40	2,67 2.5-3	6 4-7	4	0
Strychnos spinosa	0,015	11,67 10-15	4,33 2.5-7	1,67 1-2	1,67	0
Acacia rovumea	0,01	55 48-62	22,5 20-25	15 15-15	2,5	0
Neotina isoneura	0,005	13	9	4	3	0
Rinorea greveana	0,005	10	2,5	2	3	2

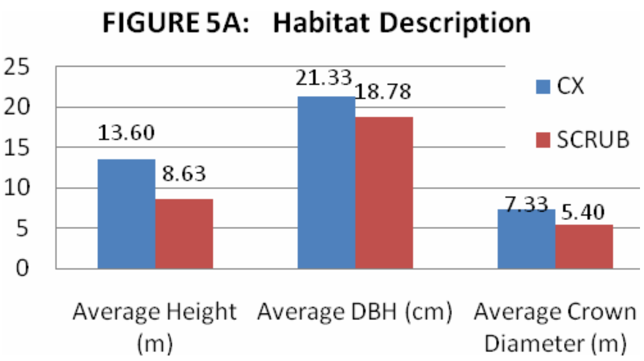
Tamarindus indica	0,005	54	25	20	3	2

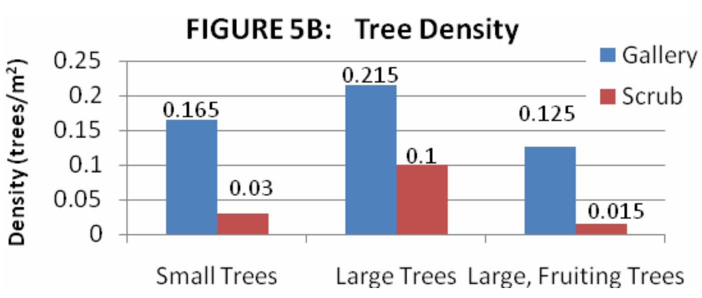
As shown in Tables 1A and 1B, the number of species representing large trees was only slightly higher in the scrub transects than in the gallery. While these results do suggest a fairly comparable degree of diversity among trees in both habitats, they remain insufficient for concluding relative breadth of food variety available to CX and Scrub Troop. As only large trees were surveyed for identification, flora diversity contributed by bushes, vines, and grasses was not quantified. Because these other forms of vegetation may serve as potential food sources for *Lemur catta*, they cannot be disregarded. Moreover, habitat evaluation revealed an acute disparity in percent ground coverage, 90 in the scrub and 12.5 in the gallery, that could indicate a higher measure of diversity among plants in the scrub habitat—See Figure 4. Average grass cover was 0.0 and 12.5 percent for the gallery and scrub habitats respectively. In addition, average undergrowth (bushes, vines, and sapling) was 55 percent throughout the scrub transects but only 12.5 percent in the gallery. Figure 4 also illustrates seventeen-fold increase in canopy cover from five percent in the scrub to eighty-five percent in the gallery. Furthermore, in 1995, the average canopy cover across the entire Malaza gallery forest was 42 percent (Blumfeld-Jones et.al., 2006). Assuming canopy cover to be an indicator of abundance of large trees and the amount of food they provide, these results substantiate the underlying claim that CX inhabits one of the most food-rich regions of the gallery forest at Berenty.

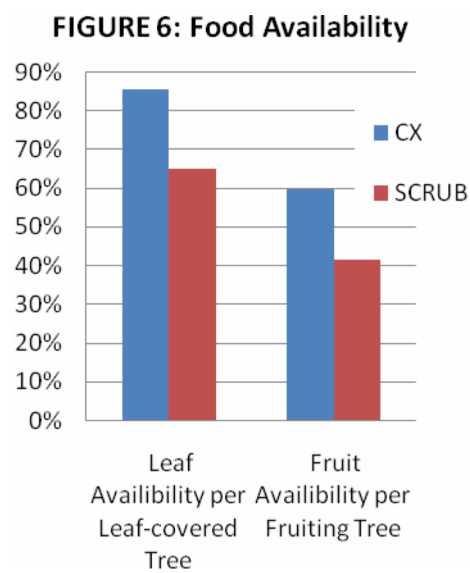
FIGURE 4: Canopy and Ground Cover



Aside from generating data on flora diversity, the habitat evaluation also provided information regarding the abundance of food sources within each troop territory. As shown in Figure 5A, the size of large trees, as measured in height, DBH, and crown diameter, was higher in the gallery than in the scrub. This difference was most pronounced in estimations of height, with the average height of large gallery trees more than 1.5 times that of large scrub trees. In addition, as both troops were frequently observed feeding on trees with DBH less than ten centimeters, it was important to note the densities of both large and small trees within each transect as well. These densities are shown in Figure 5B. Among small trees, there was a 5.5 fold increase in density from scrub to gallery. Though the disparity was less striking among large trees, it was nevertheless significant; the density of large trees in the gallery was more than two times the density found in the scrub. Overall, the higher measures of tree size and density found in the gallery lend to a greater capacity for tree-derived food sources. Furthermore, as illustrated in Figure 6, this capacity seems to be reached to a greater extent than the already smaller capacity of the scrub. With the exception of a single cactus found in the





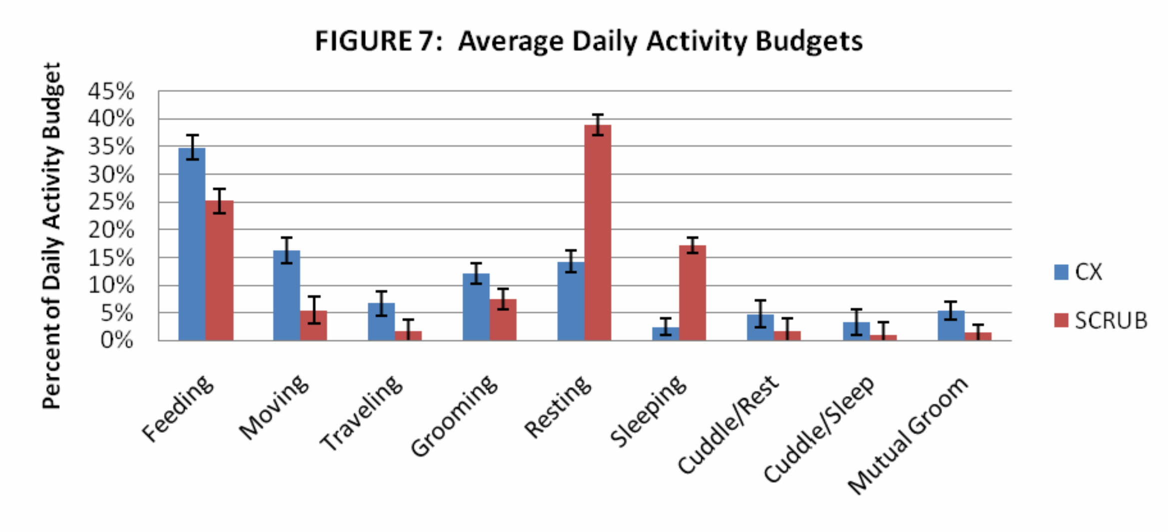


scrub, all large trees in both transects had leaves. However, leaf availability per tree differed significantly between the two habitats, from 65 percent in the scrub to 85.8 percent in the gallery. Moreover, fruit availability per fruiting tree ranged from nearly 60 percent in the gallery to just over 40 percent in the scrub. This difference is underscored by the fact that there were more than eight times as many fruiting trees found in the gallery transects as in the scrub—See Figure 5B. Thus, coupled with a greater capacity for production, the higher availability of leaves and fruits in the gallery suggests that tree-derived food sources are more abundant in the CX territory than the Scrub Troop territory.

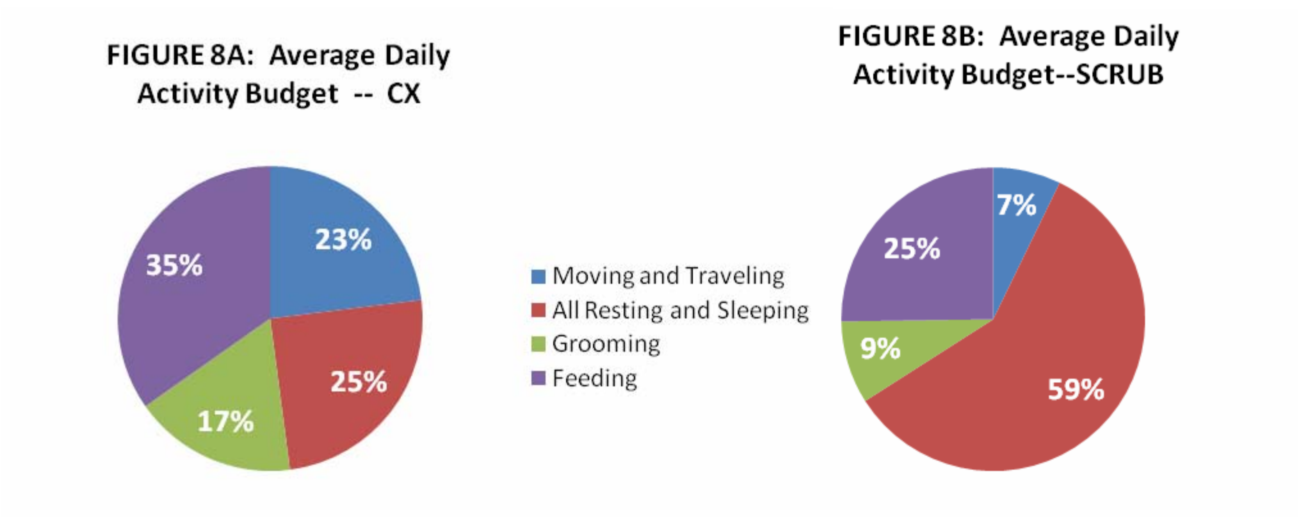
However, although undergrowth was denser in the scrub, it was excluded from the food availability evaluation; therefore, it is impossible to determine to what extent the lack of tree-derived food resources in the scrub is off-set by production of bushes, vines, and grasses. For this reason, no comparison of total food abundance is feasible. Despite this limitation and because no undergrowth in either habitat was observed to be fruiting, it is reasonable to conclude that there is a higher fruit availability in the gallery. Furthermore, the preferred food of both troops during the time of this study was *R. greveana* and *T. indica*. While densities for these two species were both only one large tree per 200 square meters in the scrub, the densities in the gallery habitat were 31 *R. greveana* trees and three *T. indica* trees per 200 square meters. In addition, the majority of the numerous small trees in the gallery transect were recognized as young *R. greveana* trees. Accordingly, it is possible to conclude that preferred food sources are more abundant in the gallery than in the scrub.

Daily Activity Budgets

Results reveal considerable differences between CX and Scrub Troop regarding both the overall activity budget and its pattern through the course of one day. Below, Figure 7 illustrates the average contribution of each observed behavior to total daily activity.

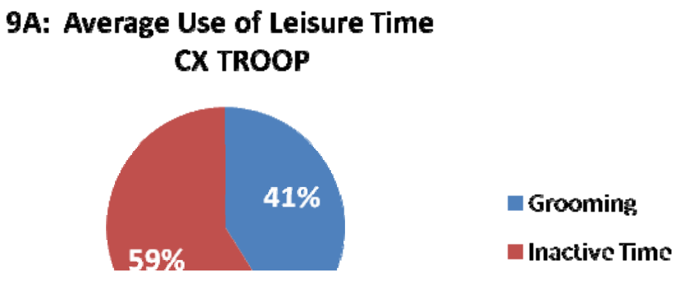


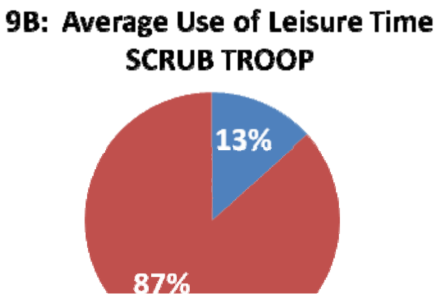
In general, the scrub troop was observed to be inactive more often and for longer periods of time than the gallery troop. This increased inactivity translated into a sizable reduction in feeding and grooming, along with an even more drastic decrease in traveling and moving. CX and Scrub Troop traveled an average daily distance of 1558. 3 and 776.1 meters respectively ($p<0.05$). Below, Figures 8A and 8B represent the average proportion of daily activity attributed to feeding, grooming, movement, and inactivity. Compared to CX, Scrub Troop spent more than twice the amount of time inactive $p<0.00001$) and less than one third of the time traveling/moving ($p<0.00001$).

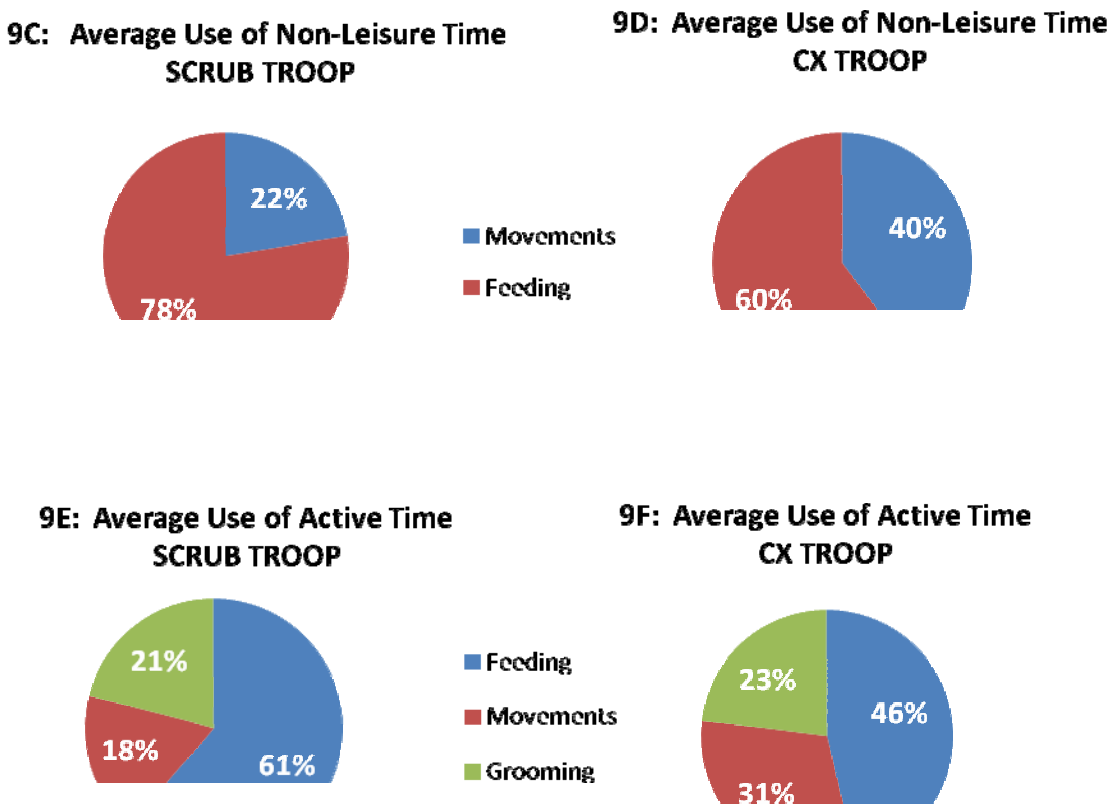


Furthermore, while inactivity and traveling/moving accounted for roughly the same fraction of the gallery troop's daily activity budget, the scrub troop remained inactive for nearly 8.5 times as long as it engaged in movement. The inter-troop disparities in time grooming ($p<0.005$) and in time feeding ($p<0.005$) were also statistically significant; CX groomed twice as much and fed almost 1.5 times as often as Scrub Troop. It is also important to note that the standard deviation in time spent feeding each day was more than twice as high among the scrub troop as CX. While feeding time in the scrub ranged between 21 and 26 percent of total activity budget for four out of the five days, one day showed upwards of 33 percent time spent feeding. This figure is much closer to the averages seen in the gallery habitat.

Below, figures 9A-F represent the component behaviors of Leisure Times, Non-leisure Time, and Active Time. As shown, CX reserved significantly more Leisure Time for grooming than Scrub Troop ($p<0.000001$). Moreover, although Scrub Troop fed less frequently than CX, they dedicated a greater percent of both Active and Non-leisure Time to feeding ($p<0.00001$ and $p<0.0001$ respectively) while CX spent more Active and Non-leisure Time moving/traveling ($p<0.001$ and $p<0.00001$ respectively). CX also appeared to groom for a greater portion of Active Time than Scrub Troop. However this difference was not found to be statistically significant.

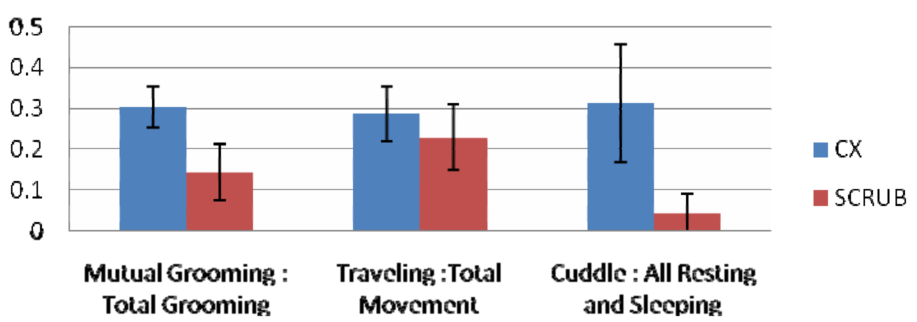






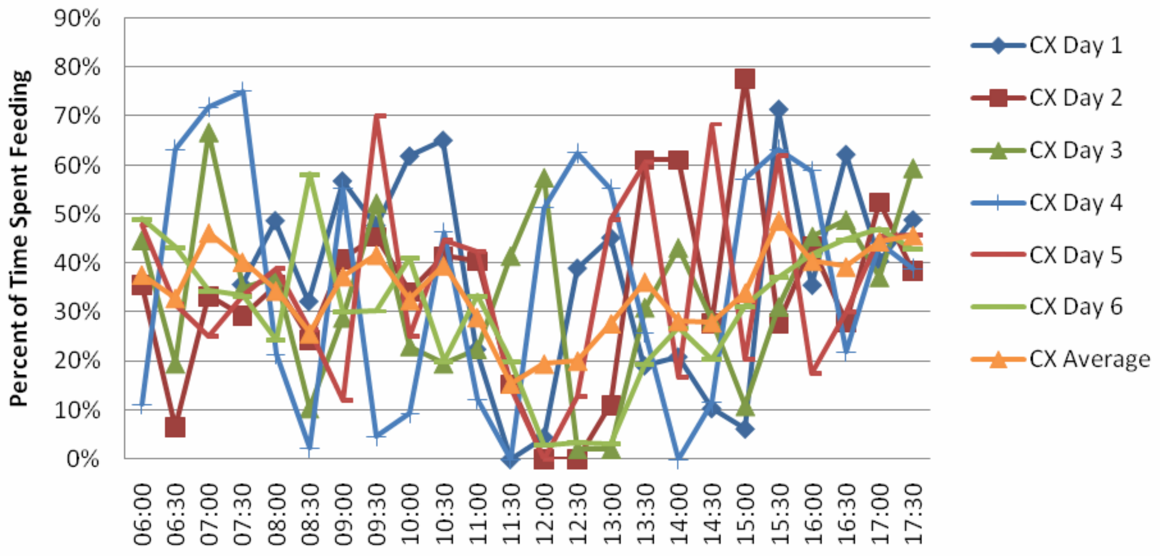
Grooming, movement, and inactivity were all analyzed for composition to generate the ratios presented in Figure 10. As shown, CX passed a substantially greater fraction of grooming time engaged in mutual grooming ($p<0.01$), and of inactive time huddled together ($p<0.01$). However, there was no significant difference between allotment of total movement to travel.

FIGURE 10: Specific Activity Budget Ratios



Aside from overall activity budget, data was also analyzed for daily activity schedule. In general, both troops remained inactive for extended periods of time around midday. However, these periods were more prolonged in the scrub, typically lasting from approximately 11h00 to 15h00. In the gallery, midday siestas were shorter and punctuated by bouts of intensive feeding. They were also far less consistent in both duration and timing. Patterns of feeding and inactivity are illustrated on pages 19-21 in Figures 11A-C and 12A-C respectively. Unlike the sharp increases and decreases in activity schedule observed among CX, the Scrub Troop's daily pattern was characterized by more gradual oscillations. Also, the daily feeding and inactivity schedules among the scrub troop were relatively consistent and therefore well-represented by the average patterns. Conversely, the erratic daily schedules of CX are poorly reflected by the average tendencies; when each thirty minute interval was averaged, the true pattern of activity was lost. This limitation must be considered when referring to the average patterns as shown in Figures 11C and 12C.

FIGURE 11A: Daily Feeding Patterns CX TROOP



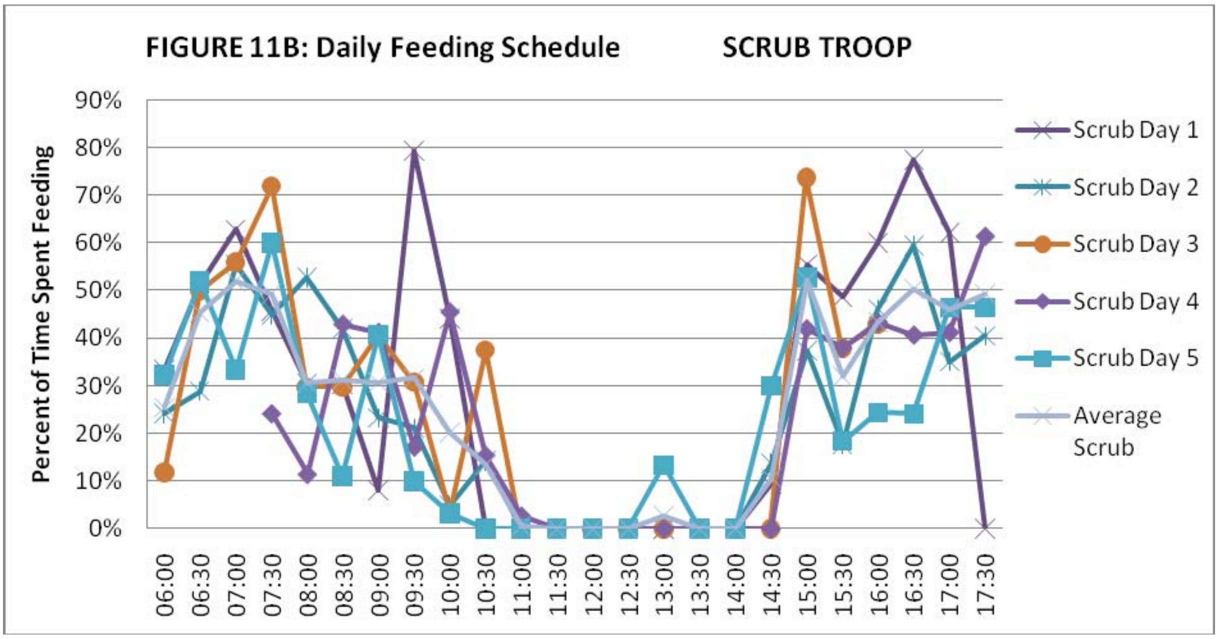


FIGURE 11B: Daily Feeding Schedule
SCRUB TROOP
Percent of Time Spent Feeding
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
06:00
06:30
07:00
07:30
08:00
08:30
09:00
09:30
10:00
10:30
11:00
11:30
12:00
12:30
13:00
13:30
14:00
14:30
15:00
15:30
16:00
16:30
17:00
17:30
Scrub Day 1
Scrub Day 2
Scrub Day 3
Scrub Day 4
Scrub Day 5
Average Scrub

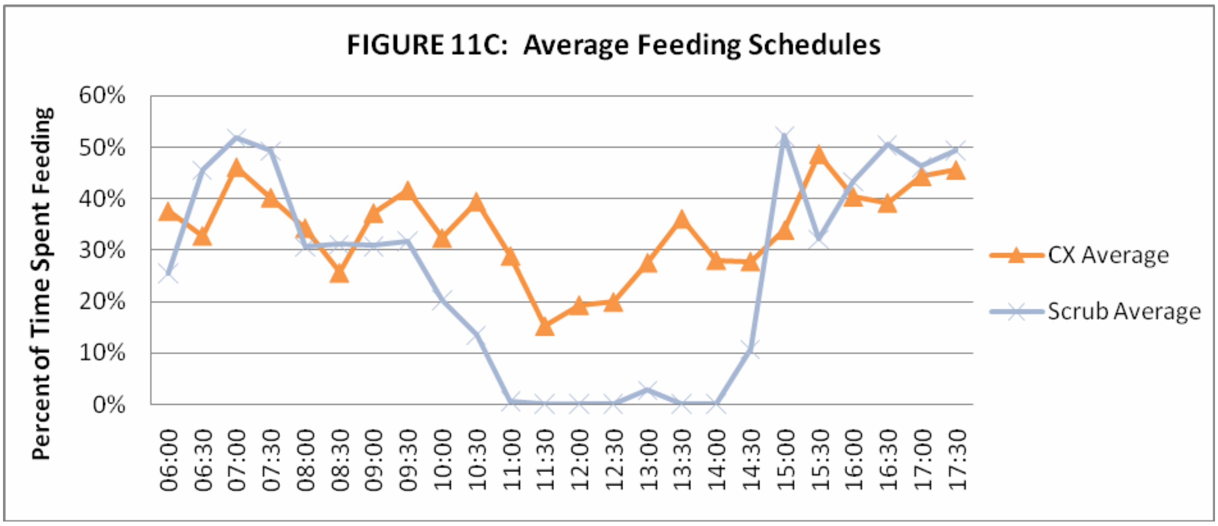


FIGURE 11C: Average Feeding Schedules
Percent of Time Spent Feeding
60%
50%
40%
30%
20%
10%
0%
06:00
06:30
07:00
07:30
08:00
08:30
09:00
09:30
10:00
10:30
11:00
11:30
12:00
12:30
13:00
13:30
14:00
14:30
15:00
15:30
16:00
16:30
17:00
17:30
CX Average
Scrub Average

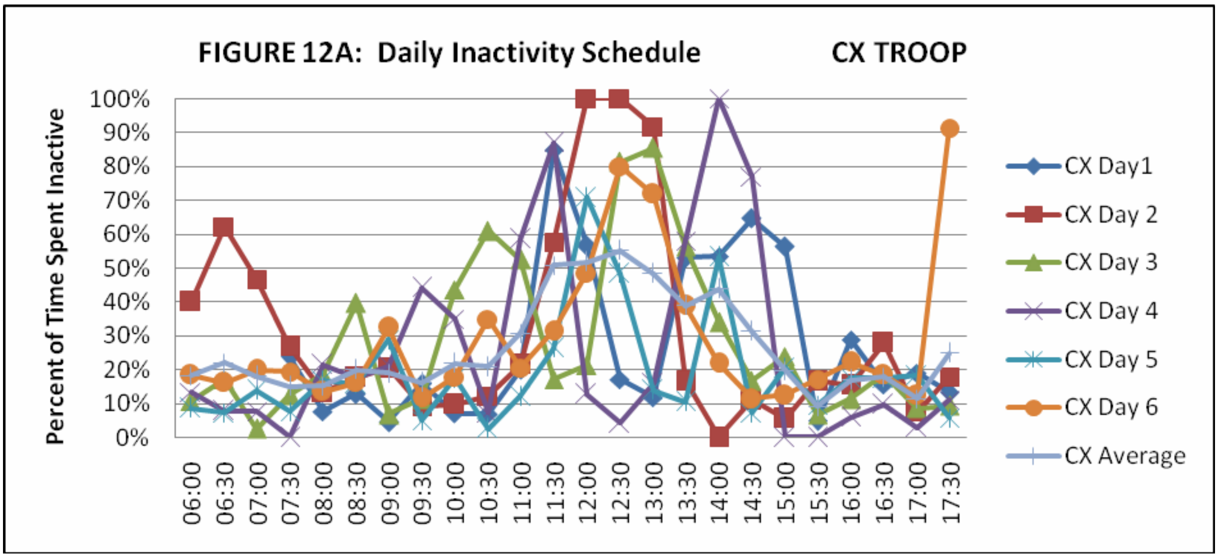
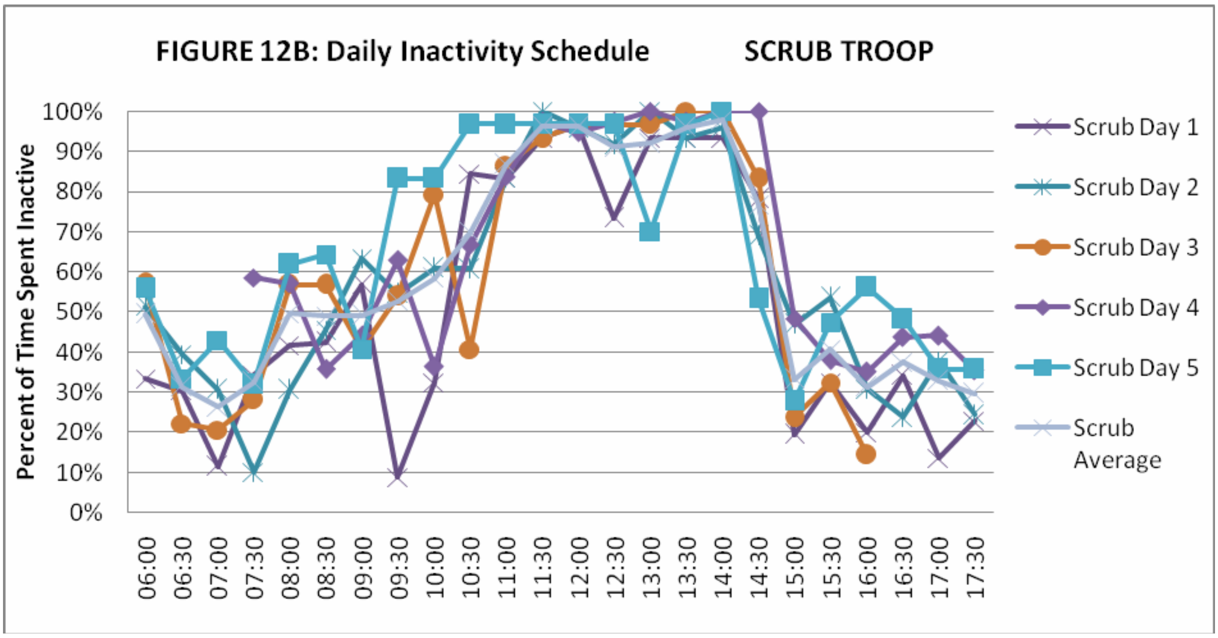
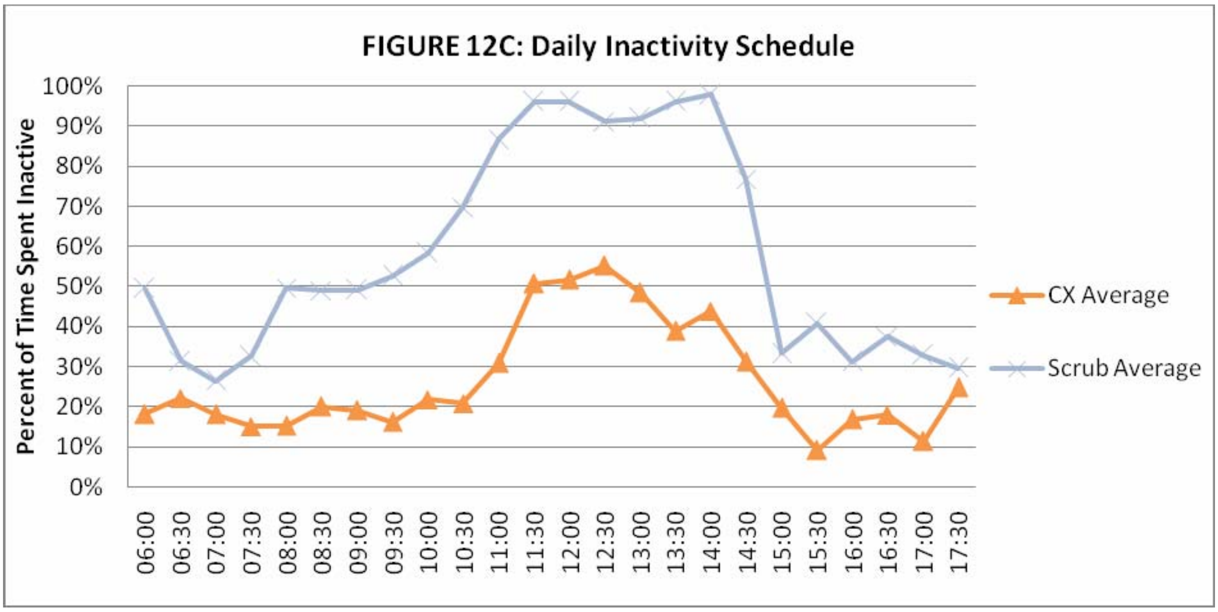


FIGURE 12A: Daily Inactivity Schedule
CX TROOP
Percent of Time Spent Inactive
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
06:00
06:30
07:00
07:30
08:00
08:30
09:00
09:30
10:00
10:30
11:00
11:30
12:00
12:30
13:00
13:30
14:00
14:30
15:00
15:30
16:00
16:30
17:00
17:30
CX Day1
CX Day 2
CX Day 3
CX Day 4
CX Day 5
CX Day 6
CX Average





Ad Libitum Social Behaviors

On average, mutual grooming was initiated more than sixty times per day in the gallery, but only sixteen times in the scrub ($p<0.001$). The greater level of variance, as evidenced by a three-fold difference in standard deviation, was observed among CX. Daily incidence of mutual grooming ranged from 47 to 81 and 7 to 18 among the gallery and scrub troops respectively.

In addition, there were 10.2 more scent marks per animal per day for CX than for Scrub Troop (p<0.001). Total daily scent marks ranged from 41 to 81 among the gallery troop and from 12 to 42 among the scrub troop. In order to avoid confounding variables related to the different gender compositions of the two groups, the average male scent marks and female scent marks were also calculated. As shown in Figure 13, inter-troop differences in scent marking, with p-values under 0.05 for males and 0.001 for females remained significant after this analysis.

Figure 13: Average Number of Scent Marks Per Day

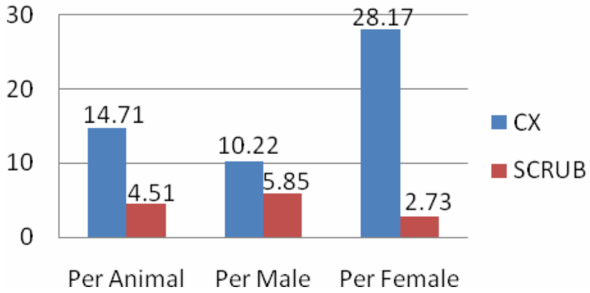
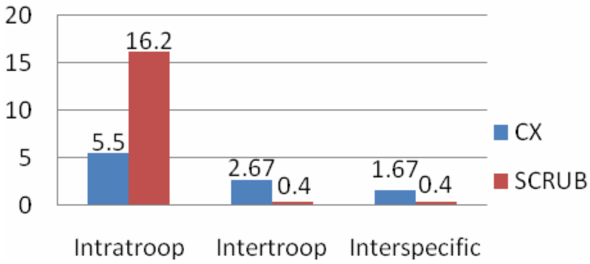


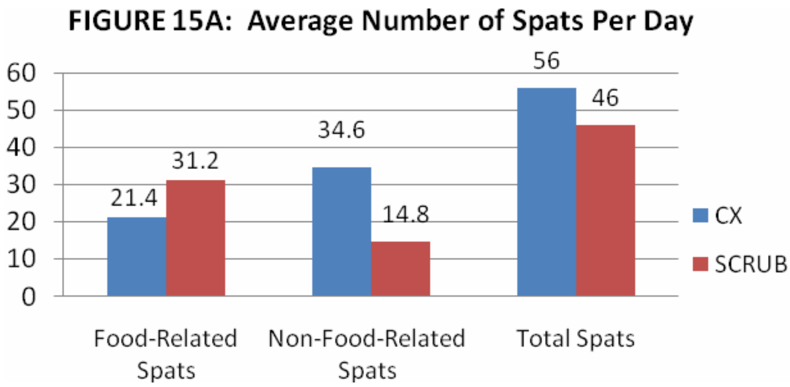
Figure 14: Average Number of Aggressive Encounters Per Day

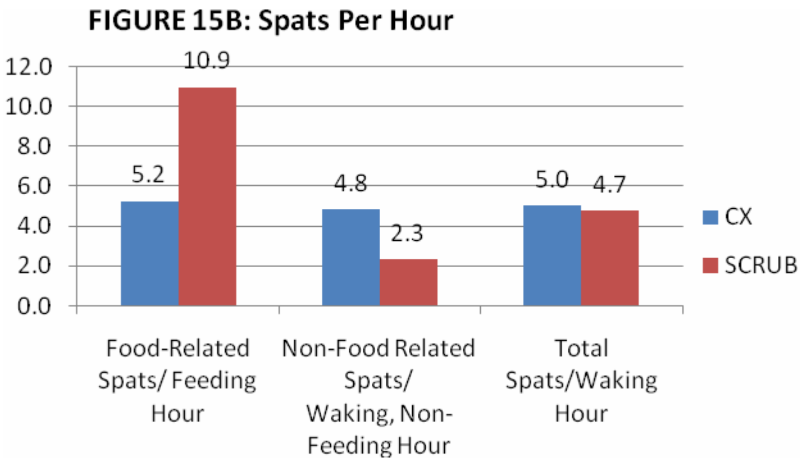


Overall, CX encountered brown lemurs 7.2 times as often and another ringtail troop 6.5 times as often as Scrub Troop. The average number of daily inter-specific and inter-troop conflicts that resulted from these encounters is presented in Figure 14. Averages for intra-troop conflict are also displayed. As shown, Scrub Troop had frequency of aggressive intra-troop encounters nearly three times higher than CX (p<0.001). Regarding inter-troop conflicts, the gallery troop exceeded the scrub troop by 668 percent (p<0.05). The difference in number of aggressive inter-specific encounters involving either brown lemurs or Sifakas was not statistically significant.

Aside from frequency of encounters, the average intensities of these conflicts were calculated, but determined to be statistically insignificant across all intra-troop, inter-troop, and inter-specific encounters. However, level three conflicts were significantly more common among inter-troop encounters in the gallery ($p<0.05$) and among intra-troop encounters in the scrub ($p<0.05$).

Regarding vocalizations of submission, spats were observed more frequently in the gallery than in the scrub. As illustrated in Figure 15, CX averaged nearly twenty more daily food-related spats and ten fewer non-food-related spats. Yet, only the difference in incidence of non-food-related spats proved statistically significant. Nevertheless, evaluating calls submission as a total daily counts introduces numerous confounding variables. In order to control for differences in activity budget, calculations were made to determine total spats per waking hour, food-spats per hour spent feeding, and non-food spats per waking, non-feeding hour. This analysis, shown in Figure 15B, eliminated statistical significance between frequencies of total spats. Remaining was a significantly greater incidence of food-related spats per feeding hour in the scrub ($p<0.005$) and of non-food-related spats per waking, non-feeding hour in the gallery ($p<0.005$). In addition, to control for other extraneous variables including individual personalities and gender composition within each troop, food-related spats were calculated as a percent of total spats and determined to be 37.8





and 67.6 percent among Scrub Troop and CX respectively. This demonstrated inter-troop disparity is of markedly high statistical significance ($p<0.0005$).

Diet Composition and Feeding Behavior

Scan counts summed to a daily average of 117.5 (range 103-130) and 44.8 (range 38-51) food patches exploited in the gallery and scrub respectively. This inter-troop disparity ($p<0.000001$) is reflected in a statistically significant difference in time spent exploiting one patch ($p<0.005$). CX and Scrub Troop averaged 2.70 and 4.14 respectively in feeding scan counts per food patch.

Across six days of scans counts, CX was observed feeding on twenty-nine varieties of food; twenty-five of which were plant species. Their daily diets encompassed between seven and thirteen food sources, with an average of 10.2. Likewise, Scrub Troop consumed a total of 30 different food sources, including 27 plant species, across five days. This translated to a daily average of twelve and a range from nine to sixteen. The inter-troop difference in daily breadth of diet was statistically insignificant; it appears that both troops exploited a comparable number of different food sources. Below, Table 2 enumerates each of these food sources, the total number of scan counts in which they were being consumed, and the corresponding percent contributed to overall diet.

TABLE 2: Food Sources Among CX and Scrub Troop

Food Sources- CX Troop	Scan Counts	Percent Total Diet	Food Sources- Scrub Troop	Scan Counts	Percent Total Diet
Azima Tetracantha	50	2,65%	*Aerva sp.*	2	0,21%
Celtis bifida	51	2,70%	*Azima tetracantha*	59	6,32%
Celtis phylippensis	4	0,21%	*Capparis sepiaria*	1	0,11%
Cordia caffra	20	1,06%	*Celtis bifida*	3	0,32%
Crateava excelsa	14	0,74%	*Celtis phylippensis*	2	0,21%
Decaying wood	12	0,63%	*Cissus quandrangularis*	2	0,21%
Dirt	32	1,69%	*Cordia caffra*	5	0,54%
Grass	3	0,16%	*Crateava excelsa*	2	0,21%
Grewia microcyclea	1	0,05%	Decaying wood	8	0,86%

Grewia salienta	2	0,11%	Dirt	19	2,04%
Hazunta modesta	3	0,16%	Fecal Matter	3	0,32%
Hyppocratea sp. (I)	5	0,26%	*Grewia microcyclea*	11	1,18%
Insects	2	0,11%	*Grewia salienta*	2	0,21%
Maeuria fififormis	1	0,05%	*Hyppocratea sp. (I)*	10	1,07%
Neotina isoneura	41	2,17%	*Hyppocratea sp. (II)*	3	0,32%
Opuntia vulgaris	27	1,43%	*Maeuria fififormis*	4	0,43%
Phyllantus spinosum	8	0,42%	*Maytenus sp.*	7	0,75%
Pisonia aculeate	1	0,05%	*Neotina isoneura*	10	1,07%
Quisivianthe papinae	4	0,21%	*Opuntia vulgaris*	16	1,71%
Rhus sp.	4	0,21%	*Phyllantus sp.*	3	0,32%
Rinorea greveana	1250	66,14%	*Quisivianthe papinae*	4	0,43%
Salvadora augustifolia	1	0,05%	*Rinorea greveana*	468	50,16%
Secamone sp. (I)	2	0,11%	*Salvadora angustigolia*	39	4,18%
Secamone sp. (II)	3	0,16%	*Secamone sp. (II)*	1	0,11%
Spiders	1	0,05%	*Strychnos spinosa*	6	0,64%
Tamarindus indica	285	15,08%	*Tamarindus indica*	229	24,54%
Terminalia sp.	6	0,32%	Unknown Bush 1	1	0,11%
Trycalisia sp.	52	2,75%	Unknown Bush 2	3	0,32%
Verbenaceae (family)	5	0,26%	*Vaughania sp.*	6	0,64%

While a similar breadth of diet variety was observed in the two troops, results indicate considerable divergence between the percent composition of each food source within the diets of CX and Scrub troop. Among both troops, *Rinorea greveana* was the species to contribute most sizably to overall diet; T*amarindus. indica* was the second most frequently consumed food source. However, as shown in Figures 16 A-B, *T. indica* is more highly represented in the scrub diet ($p<0.05$) than that of the gallery, while *R. greveana* is more highly represented in the gallery diet than that in the scrub ($p<0.005$). Furthermore, a greater fraction of the scrub diet is comprised of food sources aside from either *R. greveana* or *T. indica* ($p<0.05$).

Figure 16A: Average Diet Composition in the Gallery

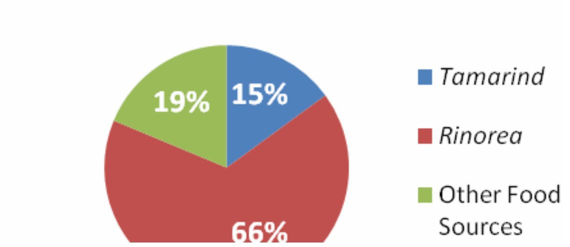
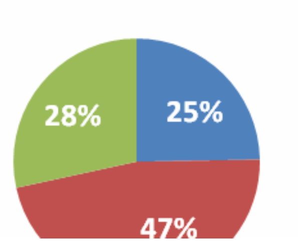


FIGURE 16B: Average Diet Composition In the Scrub



Because of inconsistencies in methodology, data concerning consumption of different plant parts cannot be quantified. Nevertheless, it is important to note that most plant species were exploited almost exclusively for leaves by both troops. Young leaves were favored where available. Consumption of buds or flowers was observed on only a handful of occasions. Both troops were observed feeding on three fruiting trees—*R. greveana*, *T. indica*, and *Crateava excels*. Among these species, the latter two were very rarely exploited for their fruits. Conversely, nearly every time a lemur was observed feeding on *R. greveana*, it was consuming fruit. Regarding broader categories of food sources, there were no statistically significant differences for fraction of bushes, vines, grass, cactus, or non-plant material represented in the diets of the two troops. On the other hand, trees accounted for a significantly greater portion of gallery diet than scrub diet ($p<0.05$); percent of trees in diet were 94.9 and 90.1 percent among CX and Scrub Troop respectively.

DISCUSSION

Overall, the results elucidate several behavioral differences between CX and Scrub Troop that are both extensive and multi-dimensional. Many of these inter-troop disparities can be explained through consideration of pressures and limitations imposed by different habitats. Selecting two troops within the same reserve allowed for circumvention of several extraneous variables pertaining to habitat composition. These variables include mega-fauna constitution, geographic location, forest degradation, and climate. Furthermore, there is a relatively low and equal risk of predation in both home ranges (Pride, 2005). Accordingly, availabilities of food and water remain as the fundamental difference between the scrub and gallery habitats. Moreover, *Lemur catta* fulfills most of its water requirement by consumption of plant material; when other water sources are unavailable or inaccessible due to territory boundaries, Ringtails are able to derive all necessary water from diets rich in succulent scrub plants (Goodman et.al., 2006). Thus, compared to food availability, proximity to the Mandrare is relegated to a minimal role in dictating Lemur catta behavior. Therefore, it is reasonable to attribute habitat-related differences among CX and Scrub Troop behavior to relative food abundance within the two home ranges.

Just as vegetation ecotones determine global *Lemur catta* range (Goodman et.al., 2006), the results of this study indicate that density and variety of flora also influence Ringtail distribution on a local scale. With decreasing food density, home ranges must increase to meet demands of minimum food intake. Therefore, occupation by CX of a smaller home range than Scrub Troop is consistent with previous reports of territory size being inversely proportional to food abundance (Anderson, 2008; Blumfeld-Jones et.al., 2006). Furthermore, larger carrying capacities of food-rich habitats can explain the higher lemur densities found in gallery forests, which average more Ringtails per hectare than any other ecosystem in Madagascar (Goodman et.al., 2006). At Berenty, although the scrub exceeds the gallery forest in area covered, the gallery has been known to support up to twice the *Lemur catta* population of the scrub (Goodman et.al., 2006). Collectively, the smaller home range of CX and evidence of higher Ringtail densities within the gallery corroborate results of vegetation analysis to confirm that food is more abundant in the gallery than in the scrub. The lower density in the scrub also explains the relative infrequency of inter-troop encounters involving Scrub Troop. Concomitantly, this decreased encounter rate lends itself to a lower degree of territoriality, an observation quantified in significantly fewer scent markings and reduced incidence of high intensity (level three) inter-troop conflict in the scrub.

Furthermore, an additional corollary of disparate food availability pertains to inter-specific encounters. The gallery, with higher food abundance and correspondingly higher carrying capacity, is a far more desirable habitat for brown lemurs than the scrub. After their accidental introduction to Berenty in 1975, the brown lemur population has been rising almost exponentially, a trend that has been largely confined to the gallery where they are better suited for inter-specific competition (Simmen et.al., 2003). Unlike naturally coexisting populations of Ringtails and brown lemurs, there is virtually no separation in feeding niche between the two species; at Berenty, brown lemurs alter their foraging style to feed on the same food sources and at the same heights as their *Lemur catta* counterparts (Pinkus et.al., 2006). Therefore, given the intensified inter-specific competition for food in the gallery, it would seem reasonable to expect a corresponding increase in aggression between brown lemurs and Ringtails in that habitat. However, although higher densities of both species rendered inter-specific encounters more frequent within the gallery, the present study found neither intensity nor incidence of aggressive conflict between the two species to be significantly higher than in the scrub. There a few possible explanations for this apparent incongruity. First, a longer study or larger sample size may have returned a significance level above five percent. An alternative rationale lies in an abundance of mutually preferred food within the gallery that is adequate for supporting both species without risk of depletion. A third and final explanation concerns novelty of competition between sympatric Ringtails and brown lemurs. As previously expounded, because these two species generally occupy separate niches, they are not natural competitors. Considering the relatively recent introduction of brown lemurs to Berenty, it is possible that Ringtail behavior has not yet adapted to recognize browns as competitors or to treat them as such.

Aside from inter-troop and inter-specific interactions, implications of food abundance also pervade the realm of intra-troop dynamics. It seems logical that lower densities of food in the scrub would increase intra-troop competition and therefore propagate tension between troop members. Moreover, lower food availabilities may give dominant females more incentive to employ aggression, enforce hierarchy, and maintain uncontested access food sources. This heightened tension may also be further exacerbated by stress associated with relative paucity of food, a factor that Pride (2005) identified as significantly correlated to cortisol levels in Ringtails. This line of reasoning explains the greater rates of intra-troop conflict, particularly those of high intensity (level three), observed in the scrub. Furthermore, scrub averages exceed those of the gallery in terms of fraction of total spats defined as food-related, and incidence of food-related spats per feeding hour. Assuming that food-related submission calls are valid indicators of food's role in reinforcing a hierarchy, these results may indicate a hierarchy in the scrub that is more intimately associated with benefits of priority feeding. Regarding the higher frequency of non-food related spats among CX, it is possible that this trend simply reflects a more stable hierarchy, one that is accepted by subordinates and maintained by their voluntary submission rather than aggressive, top-down enforcement.

Within CX, the apparent reduction of intra-troop conflict by high abundance of food may be accentuated by a heightened group cohesiveness derived from more frequent inter-troop conflicts in a more densely populated habitat. The resulting attenuation of group discord provides one possible rationale for the increased incidence of amicable social interactions observed in this troop. Compared to the scrub troop, CX spent a greater fraction of inactive time huddled together. In addition, both ad libitum tallies and scan survey counts returned a higher frequency of mutual grooming in the gallery than in the scrub. Compared to Scrub Troop, CX also spent a significantly higher fraction of grooming time engaged in a mutual grooming session; this confirms that the inter-troop disparity in mutual grooming is not simply a subsidiary consequence of increased activity among the gallery troop. Overall, a general pattern emerged that links higher food abundance to increased intra-troop amicability and inter-troop aggression. Likewise, lower food abundance correlates with heightened intra-troop antagonism and decreased frequency of inter-troop conflict.

Aside from social interactions, trends in feeding and diet can also be explained by habitat differences. In particular, effects of food density are multidimensional. Though Scrub Troop's territory is larger than that of CX, the magnitude of this difference would have to be appreciably greater in order to negate the disparity in food density between the two habitats and assign equal total food abundances to both territories. In fact, given the estimations of territory size and tree density, the scrub home range contains roughly 8,437.5 large trees and 2,531.1 small trees while the gallery contains as much as 13,571.9 and 10,415.6 large and small trees respectively. Moreover, because of the relative high risk of food depletion in territories of lower food abundance, it is necessary for scrub troops to adopt feeding strategies that conserve resources. The most obvious method is to feed less each day. Therefore, lower total food abundance in the scrub provides underlying rationale for the smaller fraction of time dedicated to feeding among Scrub Troop.

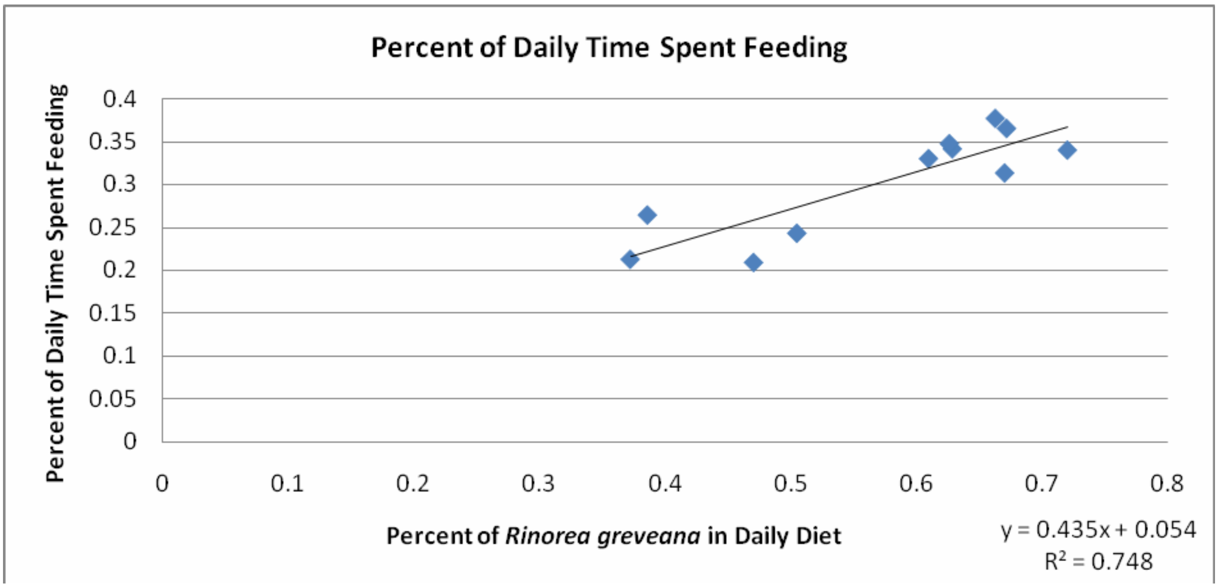
Also, inter-troop disparities in feeding pattern appear strikingly consistent with optimal foraging strategies as governed by the relative food densities in the scrub and gallery. Optimal foraging strategy relies on maximizing energy gained while minimizing energy expended. Essentially, consuming one food patch for extended periods of time results in diminishing returns in energy intake as the patch becomes increasingly depleted. In addition, moving to another parch is energetically costly. In habitats with lower densities of food, more effort is required to travel to the second patch. In habitats with higher densities of food, this energy output is of lesser magnitude and can be outweighed by the added energy input of exploiting a new, unused patch. Therefore, regardless of total time dedicated to feeding, the amount of feeding time per patch should rely on the density of available food. Troops in food-rich territories should spend less time exploiting one patch before moving on to the next; conversely troops occupying food-poor home ranges should minimize movement between patches and benefit from remaining in one patch for a greater length of time (Pyke et.al., 1977). In the present study, time feeding per patch was observed to be lower in the gallery than in the scrub. Given the higher food densities within the gallery as indicated by the vegetation evaluations, CX and Scrub Troop appear to adhere to optimal foraging requirements.

Furthermore, assuming that disparities in diet reflect the observed differences in availability of various food sources, activity budgets and schedules of both troops were likely to have been necessitated by the density, total abundance, and constitution of available vegetation. For instance, assuming the volume and energy intake of food consumption is reflected by time spent feeding, the high activity level of CX can be attributed to longer feeding times and an energy intake that is greater than in the scrub. Likewise, the prolonged periods of inactivity observed in the scrub are most likely a product of less energy in their diets. As follows, grooming and movement were more frequent in the gallery than in the scrub because both these activities are more energetically costly than feeding (Rasamimanana, 2006); CX had the internal energetic resources to expend while the energy supply of Scrub Troop was more limited. Furthermore, feeding is unlike movement and grooming in that it is the only activity that generates sizable energy input to offset energy output. As such, Scrub Troop curtailed grooming, traveling, and moving in order to focus on intensified feeding. Although overall time spent feeding was higher in the gallery than the scrub, the fraction of active time spent feeding was greater among Scrub Troop than CX. Moreover, rather than expend energy when not feeding, foraging, or ranging to feed, it appears that Scrub Troop tried to conserve energy by remaining inactive for a greater percent of their leisure time. Accordingly, the longer midday siestas in the scrub also seem indicative of efforts to maximize inactivity in order to cope with a less substantial volume of food intake in a habitat of relative food paucity. In addition, it is important to note that these lengthy bouts of inactivity coincided with the hottest time of day and that due to significantly less canopy cover, there was more direct sunlight and higher temperatures in the scrub. Therefore, desire to seek shade and escape heat was undoubtedly a contributing factor in the duration of siestas. Furthermore, the consistent timing of siestas in the scrub was an additional corollary of temperatures peaking at midday and did not allow the flexibility necessary to follow the more erratic, unpredictable activity patterns observed in the gallery.

Aside from disparities in diet quantity between the two troops, there were also significant differences in diet composition. Although the same two plant species, *R. greveana* and *T. indica*, emerged as preferred food sources, the percent of each varied between the scrub and gallery diets. This variation cannot be discounted when evaluating energy intake and its effect on activity budget. Thus far, energy intake has been assumed to be adequately estimated by time spent feeding and subsequent volume of food consumed; therefore, CX was identified as the troop with the greater energy intake. This is not problematic because, as will be shown, the differences in diet composition do not undermine, but instead confirm the assumed superiority of energy intake among the gallery troop.

Consistent with reports of November and December as the peak in *Rinorea greveana* consumption (Soma, 2006; Pride et.al., 2006), *R. greveana* dominated the diets of both troops throughout the course of this study. Specifically, this species was exploited almost exclusively for its fruit. *Tamarindus indica,* which accounts for 34.9 percent of time spent feeding each year at Berenty (Koyama et.al., 2006), was the second most represented food source in the gallery and scrub. Preferred foods are not preferred without reason; they offer something desirable to the consumer that other food sources would not. For example, *T. indica* were primarily exploited for their young leaves. Both the food availability evaluation and general observations revealed that most plant species aside from *T. indica* has only mature leaves at the time of the present study. Thus, rationale for the high percent of *T. indica* in both diets can be found in reports that young leaves contain more water, more nitrogen, fewer toxins, and fewer digestion reducers than mature leaves (Simmen & Sabatier., 1996). In terms of *R. greveana* fruit, it has been identified as a high energy, high quality food source (Pride et.al., 2006; Rasamimanana, 2006). Energy from soluble sugars can be extracted rapidly, with digestion beginning in the mouth, while fiber digestion requires symbiotic microorganisms and may take up to five hours for *Lemur catta* (JCambell et.al., 2004; Rasamimanana, 2006). Therefore, the value of fruits lies in their high concentrations of soluble sugars and low fiber content (JCambell et.al., 2004; JLambert, 1998). Leaves, in contrast, have high fiber and low soluble sugar content (JLambert, 1998). Furthermore, because of high levels of pectin and gum, the fiber that is contained in fruits is largely soluble fibers; conversely, leaves have a greater fraction of insoluble fibers, which are considerably more difficult to digest (JCambell et.al., 2004). In addition, prosimians are caeco-colic fermentators. Essentially, this translates to a maximal energy intake when diets are high in soluble sugars and low in fibers (JLambert, 1998). In summary, it is clear that *Lemur catta* benefits from consumption of fruit. Because *R. greveana* was the only species at the peak of it fruiting season, the fruit of *R. greveana* was an obvious choice for a preferred food.

Moreover, CX ate significantly more *R. greveana* as a fraction of total diet than Scrub Troop. Therefore, it appear that the higher energy intake in the gallery was due not only to volume of food consumed, but also to the composition of diets. Attesting to this fact are reports of longer midday siestas among troops with low quality diets (Pride et.al., 2006). As a result of higher energy intake; CX had more energy to expend on feeding and other active pursuits. On Day One of Scrub Troop follow, the troop was observed to spend an amount of time feeding that more closely resembled overall patters in the gallery than those in the scrub. Also, the Scrub Troop diet for Day One was comprised of a percent *R. greveana* that was much more characteristic of CX. This suggests, as shown below, positive correlation between the fraction of *R. greveana* in a diet and length of time dedicated to feeding.



Although this study returned reasonable and statistically significant results, there are limitations to consider. The majority of these limitations can be attributed to time constraints that prevented a comprehensive investigation. The most pervasive inadequacy is insufficient data on food available to each troop. An analysis of energy and nutrition offered by different food sources would have eliminated considerable speculation. Also, undergrowth should have been assessed for food availability. In addition, more transects for density and phenology should have been done to demonstrate relative variability of food abundance within a home range. Furthermore, conducting only one transect in each habitat may have introduced skewed results if the chosen transect was not completely representative of the overall home range. This was particularly problematic in the scrub where food availability is patchy and no one transect is capable of presenting an accurate indication of food abundance. Another significant limitation was the small sample size. Only two troops, one from each habitat type, were observed. Thus, individual personalities within the troops could have certainly skewed the data. Using a greater number of troops to represent each habitat would have circumvented this issue. Furthermore, it was not possible to find a troop from the scrub matched to CX in size and gender composition. Therefore, the difference in number of males and females per group could have certainly confounded the data, particularly the data on social interactions. In terms of methodology, there were two other limitations that merit discussion. First, quantifiable data on consumption of plant parts was inconsistent; therefore analysis relied on general observation and incomplete data collection. Secondly, it would have been interesting to distinguish between foraging and feeding during the scan counts to further investigate any possible inter-troop differences in foraging.

CONCLUSION

Considering the differences observed in the gallery and scrub, it appears that multiple facets of Ringtail behavior can be attributed to environmental influences. In particular, disparities in vegetation density and composition within a habitat seem to underlie inter-troop variations in activity budget, social interaction, and foraging strategy. Thus, this study supports the conclusion that behavior among *Lemur catta* is inextricably tied to relative food abundance, particularly that of preferred food sources. However, because of the substantial limitations of this study, it should be considered preliminary and is inadequate to ascertain any definitive conclusion. Longer studies involving more troops and a third habitat would be ideal; more vegetation analysis would be imperative. Nevertheless, this study does indicate that the effects of quality and quantity of available food may be extremely significant in determining behavior and therefore merits further investigation.

If additional studies do corroborate the results presented here, there could be extensive implications that encompass both the past and the future. Regarding the past, a deeper knowledge of the correlation that links prosimian behavior with the quantity and composition of diet could be valuable for interpreting the primate fossil record. Combining fossil evidence of diet and habitat, tentative inferences could be made concerning the foraging strategies, activity budgets, and social interactions of extinct primates. In addition, among the future implications is one that pertains exclusively to Berenty. In the reserve, there is a well-documented trend of drying in the forest. From 1973 to 2000, the canopy cover in the gallery was reduced by fifty percent and the vegetation ecotones of Malaza moved towards the river, resulting in scrub habitat encroaching on the gallery (Blumfeld-Jones et.al., 2006). Furthermore, the increasing population of brown lemurs, which dominate over Ringtails as inter-specific competitors

(Pinkus et.al., 2006), and the appreciable decrease in *T. indica* density suggest a decline in food availability in the gallery(Blumfeld-Jones et.al., 2006). As such, it appears that the gallery is becoming increasingly similar to the scrub habitat in canopy cover, food availability, and vegetation composition. Moreover, the present study indicated that these elements of habitat have extensive influence on *Lemur catta* behavior. Therefore, it may be possible to use the observed behavior of the scrub troop to predict the future direction of Ringtail behavior in what is now the gallery forest of Malaza. This possible difference in future behavior may have pervasive consequences in the realm of ecosystem dynamics. On a more global scale, the value of the present study lies in its identification of behavioral adaptations to life in a naturally food-poor habitat. These adaptations may elucidate behavioral mechanisms employed by Ringtails to cope with unnaturally low food availability in degraded forests. This would be an interesting angle for future study.

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