AN EVALUATION OF THE NATURAL AND PROVISIONED FEEDING RATES OF SEMI-FREE RANGING RINGTAILED LEMURS (*LEMUR CATTA*) ON ST. CATHERINES ISLAND, GA

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CHAPTER I

INTRODUCTION

Feeding Ecology

Primatology is a young discipline and its methodology in the 1950s and 1960s was mainly descriptive. Early primatologists used a natural history approach in their studies and focused on the social behavior of just a few species; namely, baboons (*Papio* spp.), macaques (*Macaca* spp.) and howler monkeys (*Alouatta* spp.) (Sussman, 1999). In contrast, primatologists currently use a problem-oriented approach that encompasses a range of primate species and includes an emphasis on ecological issues. The inclusion of ecology in primatological studies of wild and semi-free ranging species is necessary as social behavior is influenced by habitat; thus, social behavior and ecology are interrelated and must be considered in tandem. The study of primate ecology originated from Carpenter's (1934) work on howler monkeys, but it has only really developed since the 1960s following the expansion in primate field studies (Chivers, 1986). By the 1970s, researchers began to focus on problem-oriented field studies: determining relationships between behavior and morphology, ecology and social structure, and community interactions (Sussman, 1999).

According to Chivers (1986), ecological study usually involves some aspect of feeding behavior. For example, he states that quantitative descriptions are needed of the following: (1) plant species composition, distribution and abundance, (2) food selection

at different times of day, month, and year, and (3) all aspects of foraging and ingestive behavior. Such information is then compared with group size and composition, activity budgets and patterns, and intra/inter-specific interactions. Data on primate diets are usually from feeding percentage studies since they are the most accessible information to field researchers. In addition to calculating feeding time rates, it is important to conduct nutritional and secondary compound content analyses on natural foods. Such analyses can help primatologists to understand why primates have such a varied diet, why primates eat certain plant parts, and the change in foraging strategy when fruit is scarce. Further, these data allow primatologists to formulate ecological strategies of various species and help them understand the relationship between foraging strategy and various aspects of social behavior such as social structure.

Description of *Lemur catta*

Taxonomy

Lemur catta is taxonomically categorized into the suborder Strepsirhini, which also includes lorises. The strepsirhines are the most primitive of the two suborders (the other being the Haplorhini, which includes tarsiers, monkeys, apes, and humans) because they have retained many of the morphological characteristics that their primate ancestors had 40 to 50 million years ago (Fleagle, 1999). Lemurs, however, have diversified immensely and filled numerous ecological niches largely due to their isolated status on the island of Madagascar (Richard and Dewar, 1991; Goodman and Benstead, 2003; Gould and Sauther, 2006).

Madagascar

Lemurs are endemic to the island of Madagascar. Madagascar, the fourth largest island in the world, is situated to the southeast of Africa and is separated from the continent by the Mozambique Channel (Swindler, 2002). It has been estimated that Madagascar reached its current position, 800 km from Africa, 120 million years ago (Rabinowitz et al., 1983). The reason for the predominance of primates on the island is unclear, but it is possible that the ancestors of lemurs successfully rafted from the African mainland, whereas other mammals were unable to do so (Richard and Dewar, 1991). Regardless of the ancestral origins of lemurs, the diversification of the lemurs was favored by the various environments and flora types on the 590,000 km^2 island and the lack of competition from other mammal species (Richard and Dewar, 1991).

Today, ringtailed lemurs are restricted to the south and southwestern portions of Madagascar. Ringtailed lemurs inhabit areas within and around nine forests that contain nine other lemur species. However, most research has been conducted at the Beza Mahafaly Special Reserve and the Berenty Primate Reserve (Cawthon, 2005). In the most southeastern portion of the ringtailed lemurs' range, they live at an elevation range from sea level to 2,600 m and in a variety of habitats: rainforests, deciduous, gallery, subalpine, and spiny bush forests (Goodman, 2003). In southwest Madagascar, desert or thorny scrub habitat is prevalent and the area has been subject to periodic drought, which has seriously impacted populations of *Lemur catta* (Gould et al., 1999; Jolly et al., 2002; Cawthon, 2005).

Morphology

Within the family Lemuridae, *Lemur catta* is undoubtedly the flagship species (Mittermeier et al., 1992). *Lemur catta* has been chosen to represent the family Lemuridae to promote public awareness and support for conservation in Madagascar due to its vulnerability, distinctiveness, and even its attractiveness. The striking characteristic for which *Lemur catta* is known is their long tail that has alternating bands of black and white. The sexually monomorphic ringtailed lemur, weighing an average of 2.2 kg in the wild, is the most terrestrial of all lemurs. Both males and females have anogenital scent glands, but only males have scent glands on their chests and on the inside of their wrists (Cawthon, 2005).

Social Structure

Ringtailed lemurs live in multi-male groups, ranging from 5-27 individuals, with approximately 1:1 sex ratios (Sussman, 1977). A dominance hierarchy exists within groups of ringtailed lemurs and adult females are dominant to males (Jolly 1966). Most females remain in their natal group and males usually emigrate once they reach adulthood (Jones, 1983; Sussman, 1992). Males will emigrate from their natal group being unable to mate with most of the females from their natal group due to their relatedness and female inbreeding avoidance behaviors (Taylor, 1986; Sussman, 1999).

Feeding Ecology

Modern field research on lemurs was first conducted by Jean-Jacques Petter (1962; Sussman, 1999), who carried out surveys and noted the ecology and behavior of several different species of prosimians in Madagascar. At Berenty Primate Reserve, Alison Jolly (1966) was the first researcher to conduct an intensive field study of *Lemur*

catta. Comparative studies of *L. catta* were carried out in western Madagascar (Sussman, 1972), and long-term research was initiated at the Beza Mahafaly Reserve in the southwest in the 1980s (e.g., Richard et al. 1987, Sussman 1991; Sauther, 1992; Gould 1994). Such research has included ecological studies on ranging patterns, diet and foraging behavior, activity cycles, and social structure and organization.

As mentioned earlier, ringtailed lemurs occupy a variety of habitat types, with the western and eastern portions of Madagascar having their own distinctive climate and vegetation (Cawthon, 2005). Thus, ringtailed lemurs inhabit a highly seasonal and variable environment, of which they must exploit a large array of food sources throughout the dry and rainy seasons. In general, the diet of ringtailed lemurs has been studied extensively in the gallery, riverine, closed canopy, and opened forests, but there is little published information regarding the plant species fed on in the dry spiny forest or the montane areas of Madagascar (Simmen et al., 2006). Ringtailed lemurs are considered to be opportunistically omnivorous, although they focus their feeding on ripe and unripe fruits, young and mature leaves, leaf stems, and seeds (Jolly, 1966; Sussman, 1977). On rare occasions, they have been observed to eat exudates, invertebrates such as spiders and grasshoppers, and birds (Sauther et al., 1999; Jolly, 2003). One of the most important food sources for ringtailed lemurs is the abundantly distributed tamarind or kily tree (*Tamarindus indica*), which produces edible parts, namely fruits and leaves, throughout the year (Jolly et al., 2002). In fact, during the dry season months of May through September, the kily tree is one of the only fruit sources available to the lemurs (Sauther, 1998). However, over an entire year, two groups of ringtailed lemur at Beza Mahafaly fed on approximately 50 species of plant (Sauther, 1992) and the number of

plant species fed upon varied within different sites, seasons, and even sex (Sauther, 1993). For example, dietary differences have been shown to exist between males and females during lactating and mating seasons. Dietary differences have also been found between groups at Berenty and groups at Beza Mahafaly greatly due to the availability of many more introduced plant species in the former site, along with food and water provided by humans (Simmen et al., 2006). For example, while the kily tree still remains a keystone resource, many lemur groups in Berenty have shifted from kily mature leaves to leaves of an introduced leguminous tree (Soma, 2006).

According to Sussman's (1977) comparative study of *Lemur catta* and *Eulemur fulvus*, or the brown lemur, at Berenty, Tongobato, and Antserananomby, ringtailed lemurs had a more varied diet with 45 plant species compared to 13 plant species for *E. fulvus*. Sussman (1977) concluded that ringtailed lemurs' varied diet was related to their foraging pattern for several reasons. Compared to *E. fulvus*, ringtailed lemurs had a diverse vertical and horizontal ranging pattern by utilizing all the forest levels, and they spent the majority of their time feeding in the lower levels between 0-7 m. *L. catta* traveled more extensively than *E. fulvus*, with a day range of approximately 1,000 m, and would visit their total home range within seven to ten days. Lastly, *E. fulvus* was cathemeral while ringtailed lemurs were diurnal with morning and evening peaks of activity. In general, the extensive travel of ringtailed lemurs allows them to "use resources as they become available so that the food species can change dramatically from month to month" (Simmen et al., 2006: 61).

With information from field studies in hand, several researchers have investigated *L. catta* feeding ecology in semi-free ranging conditions. Research on feeding behavior of

primates in laboratory and other captive contexts has had similar goals of discerning food selection, foraging strategies, and digestive capabilities (Chivers, 1986). Captive studies offer the advantage of better observation conditions, the individual histories of the study subjects are known, and researchers have greater control over the social and physical environments. Ganzhorn (1986), for example, studied the feeding ecology of sympatric groups of ringtailed and brown lemurs at the Duke University Primate Center (DUPC) in North Carolina (renamed the Duke Lemur Center). Both species were housed within a 0.5 ha enclosure in a mixed pine forest at DUPC, were provisioned daily with primate chow and fruit, and were allowed to range freely throughout the enclosure. The purpose of Ganzhorn's study was to assess the influence of plant compounds on natural food selection by *Lemur catta* and *E. fulvus*. He compared the seasonal availability of native food from winter to summer, estimated the amount of food eaten per animal per day, and performed chemical analyses on 74 parts of 24 different plants for compounds such as fiber, alkaloids, and tannins. Ganzhorn (1986) found that ringtailed lemurs chose plant items according to their availability in the winter, but not necessarily in the summer. While *Lemur catta* food choice was partially influenced by the availability of different plant items, food choice was not based on nutritional importance since no correlation was found between food choice and nutrient composition.

Ringtailed lemurs have also been introduced and established as a semi-free ranging breeding population on St. Catherines Island (SCI), Georgia and several researchers have studied them since their release in June, 1985. Keith-Lucas et al. (1999) conducted research on the ringtailed lemurs following their successful release in order to examine whether the captive-reared and developmentally deprived study subjects could

develop species-typical social and ecological behaviors in their new setting. Keith-Lucas et al. (1999) noted the ringtailed lemurs' progressive changes in physical condition, activity patterns, ranging patterns, vocalizations, social organization, and foraging behavior. Dierenfeld and McCann (1999) collected data on the natural feeding behavior of *Lemur catta* on SCI. Their observations were conducted seasonally at quarterly intervals (February, May, August, and November) for one year, and chemical assays of the native plant species consumed by the animals were conducted to determine nutrient composition (protein, fiber, carbohydrates, and fats) of the plants. Finally, in a more recent study of the feeding behavior of the ringtailed lemurs on SCI, Savage (2005) collected data on four groups of ringtailed lemurs to determine relationships between activity budgets, home range size, habitat quality, and provisioned feeding and foraging rates.

In addition, I investigated the feeding behavior of one troop of ringtailed lemurs on SCI from August to December 2006 to contribute information to the island's feeding ecology database. While previous studies included information on the natural foods foraged by the lemurs on SCI, feeding sample times were too few to provide a detailed assessment of the various species consumed by *Lemur catta*. Therefore, the purpose of my study was to conduct a more thorough investigation of forages and to provide baseline data for future studies of *Lemur catta* nutrition on SCI. In addition to a daily provisioned diet, which consists of a commercial primate biscuit and a variety of produce, the lemurs have unlimited access to native flora and fauna (Dierenfeld and McCann, 1999). Although several studies have recorded plant resources foraged by the lemurs on SCI (Dierenfeld and McCann, 1999; Keith-Lucas, 1999; Savage, 2005), most

of those forages fruit and flower in the spring and summer. My study mostly took place during the fall and the availability of natural fruits and flowers was limited. In addition, SCI has a low floristic density compared to that of neighboring barrier islands along the coast of Georgia, and is, predominately, an oak and pine forest (Coile and Jones, 1988). This gave me the opportunity to see what low quality natural foods the study subjects might use. Some researchers consider ringtailed lemurs to be a "weed" species that is well adapted to boom and bust conditions (Gould et al., 1999). This means that they should be able to subsist on low quality foods and exploit less desirable habitats. Data on the feeding bouts of ringtailed lemurs are presented herein and have been used to largely determine: 1) the percentage of feeding time of natural foods compared to provisioned feeding, 2) the degree of preference in non-provisioned dietary items, and 3) whether there are any differences in feeding due to age or sex. Furthermore, the unexpected introduction of two captive adult males previously unfamiliar with natural settings provided me with an opportunity to investigate how quickly the newly introduced males transitioned from provisions to including natural forages in their diet. In addition to this particular comparison between new adult members and their experienced free-ranging group members, dietary differences between sexes have not previously been investigated on SCI and may give insight as to whether the lemurs exhibit species-typical feeding behavior.

CHAPTER II

METHODS

Study Site

In June 1985, ringtailed lemurs were introduced and established as a semi-free ranging breeding population on St. Catherines Island (SCI), Georgia, USA. SCI is a barrier island off the coast of Georgia that is approximately 57.8 km^2 in size and consists of a mixed deciduous and evergreen forest, palmetto, savanna, and both fresh and saltwater marshes (Thomas et al., 1978). A captive-born *L. catta* group was released, with support by the Wildlife Conservation Society, in June 1985 in the northern portion of the island (Keith-Lucas et al., 1999). The introduction of ringtailed lemurs on SCI was launched for field research purposes and for the future possibility to restock populations in Madagascar (Iaderosa and Lessnau, 1995).

When I began my study, three ringtailed lemur troops with approximately 30 individuals total were ranging on the northern portion of the island. Each troop has its own feeding site/enclosure in which it is provisioned daily with primate chow and fruits. The three feeding sites are situated roughly between one-half and one km apart from each other. I conducted my study on only one of three groups on the island, "Group 3." I chose this group due to its greater number of individuals, juvenile to adult ratio, and male to female ratio. In addition to calculating feeding percentage times, data on feeding bouts

were used to determine differences between sex and age in food intake.

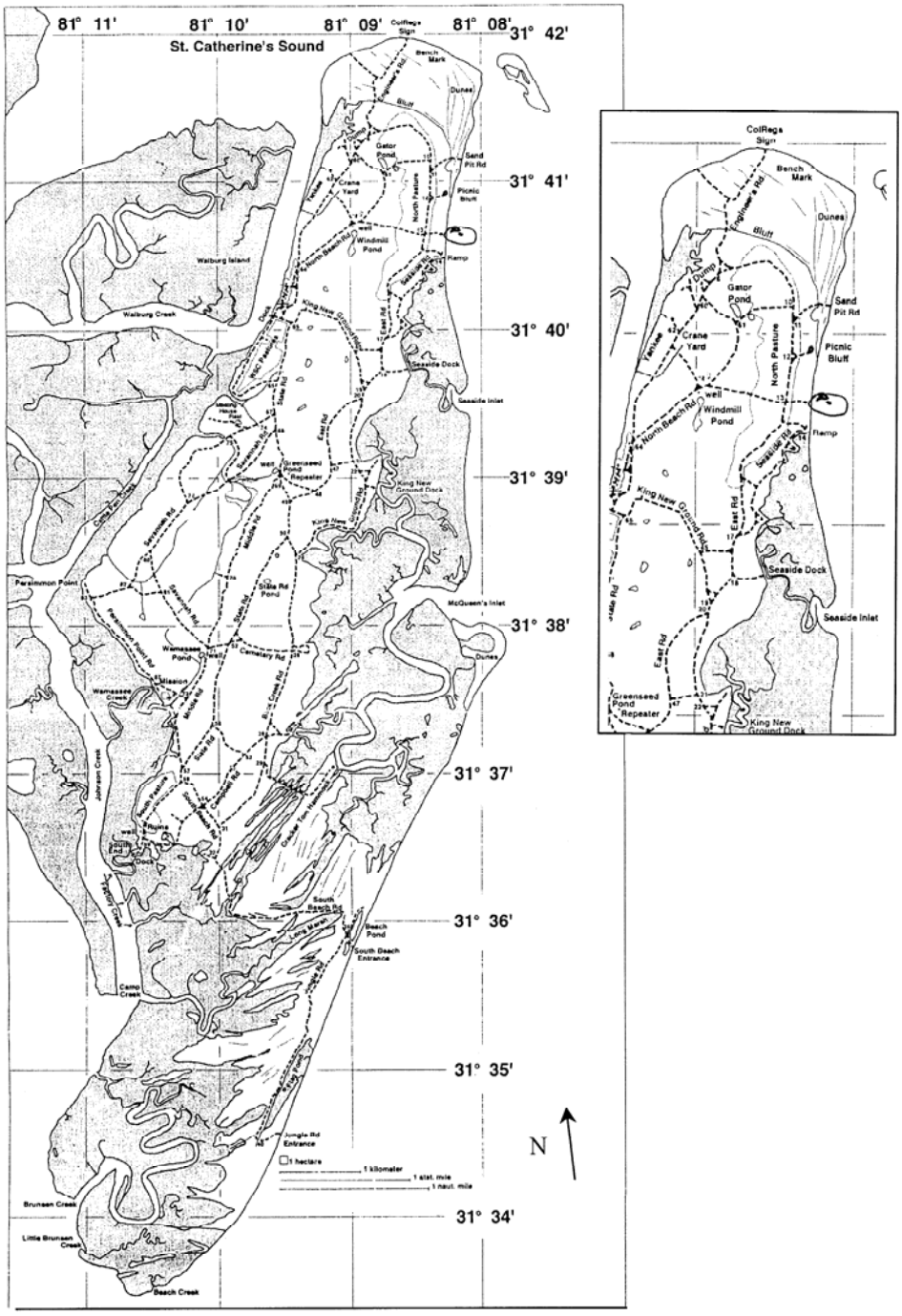

Figure 2.1: Map of SCI Modified from Keith-Lucas (2001)

Group Composition and Data Collection

I collected data on all juvenile (1 year) and adult (2 years +) ringtailed lemurs between August 24, 2006 and December 13, 2006 using focal animal sampling (Altmann, 1974). Each individual in the study group was recognizable by a collar and/or by idiosyncratic features (e.g., markings on face, tufts of ear hair, tail length). My focal group contained nine to 11 study subjects: five adult females (mean age: 6.4 years, range: 2-12 years), three juvenile females (1 year), one juvenile male (1 year), and two adult males (both aged 13 years). The variation in study group size is due to the removal of one adult male, the introduction of two adult captive males to the group, and the death of an adult male. The original adult male, Minter, was removed from the group on my third day of sampling for colony management purposes and was therefore excluded from this study. Minter had been in this particular group since June 2001 (Lessnau, personal communication), and the SCI staff primatologists remove adult males and bring in foreign males in order to reduce inbreeding. Two captive adult males, Nick and Pan, were brought to the group's feeding site on August 29, 2006, but the males were not allowed to range with the rest of the group until October 6, 2006. The staff primatologists conducted a soft release, in which these males would interact with a few members from the group during daily provisioned feeding within the confines of the feeding enclosure. Due to late introduction of the adult males to the group, I only sampled adult females and juveniles between August 24, 2006 and October 17, 2006.

Keith-Lucas et al. (1999), the first researchers to collect data on the ringtailed lemurs on SCI, made the observation that the lemurs were most active around sunrise and sunset. Therefore, I usually collected three hours of data on one focal animal in the

morning (earliest start time of 6:55 and latest stop time of 12:44), and another three hours in the late afternoon (earliest start time of 14:00 and latest stop time of 19:36). I conducted six one-hour focal observations each day. I categorized each hour as follows: M1 for the first morning hour, M2 for the second morning hour, and M3 for the third morning hour (the same applies for A1, A2, and A3 for the afternoon hours). Focal animals were selected randomly for both morning and afternoon, and total sample times were balanced between group members and time of day. If I did not conduct exactly three one hour focal samples in the morning, it was because I was unable to find the lemurs early enough. For example, one morning I found the group at approximately 10:00, the lemurs were provisioned at 11:00 and asleep before 12:00. Therefore, I sampled the focal animal for only two hours and categorized the hours as M2 and M3. If I did not conduct exactly three one hour focal samples in the afternoon, it was because the group moved too quickly through largely impassable walking areas. Once I traveled around large pools of water or through thick brush, the lemurs were out of sight and I was unable to locate the group. Such instances occurred rarely. I coincided the end of the last hour with sunset because soon after sunset, I was unable to clearly recognize individuals in the group. The last focal sample, A3, usually ended between 18:45 and 19:15. Data were collected four to six days per week, on average.

My arrival time at the group's feeding site was approximately one half hour before sunrise (arrival time ranged from 6:30 to 7:00). Although a radio transmitter/tracker was used to locate a radio-collared individual from the group, the time that I first saw the group each day varied slightly as the group was not always in the same location I left it in the previous evening. Once I located the group, I immediately began

recording data on the focal animal for that morning. In addition, I attempted to coincide the last morning sample (M3) with provisioned feeding. This proved to be difficult due to the variation in provisioned feeding.

The following data were collected during each focal animal sample. (1) The beginning and end time of all feeding bouts (> 10 seconds), feeding height (categorized into varying height levels from the ground: 0-5, 6-10, 11-15, and 15+ meters), and if applicable, bite counts (i.e., the number of handfuls or mouthfuls) of food items were recorded using a hand counter. (2) The type of food was recorded (e.g., provisioned fruit/primate biscuits or native flora and fauna), and if visible, the part of the native plant ingested. The phenophase of ingested native flora and fauna was characterized as ripe fruit, unripe fruit, seeds, new leaves, mature leaves, flower buds, flower parts, insects, soil, and other miscellaneous wild food items (e.g., mushrooms and fungus). An example is provided below (Table 1.1). Photographs and descriptions were taken of all native flora and fauna eaten by the study subjects for later identification.

Table 2.1: Afternoon Sample Example

Focal: Becky		Start: 14:15	Stop: 15:15		Date:	11/15/06
Time (seconds)	**Genus**	**Species**	**Part**	**Phen.**	**Height**	**Bites**
450	*Provisioned*	*food*	N/A	N/A	1.5 M	15
150	*Pinus*	*palustris*	Seed	N/A	0 M	11
45	*Pterocaulon*	*pycnostachyum*	Stem	N/A	0 M	5
64	*Soil*		N/A	N/A	0 M	N/A
234	*Sabal*	*palmetto*	Fruit	Ripe	5 M	38
Total time:	943					
% feeding:	26.19					
		Start: 15:30	Stop: 16:30			
77	*Quercus*	*virginiana*	N/A	N/A	9 M	4
57	*Pinus*	*taeda*	Seed	N/A	0 M	4
Total time:	134					

Table 2.1-Continued

% feeding:	*3.72*					
		Start: 16:30	Stop: 17:30			
789	*Sabal*	*palmetto*	Fruit	Ripe	7 M	137
289	*Sabal*	*palmetto*	Fruit	Ripe	7 M	N/A
120	*Quercus*	*virginiana*	N/A	N/A	10M	N/A
Total time:	1198					
% feeding:	33.28					

These data were used to calculate feeding rates (time spent feeding/total time observed), the amount of time spent feeding on a particular food type (e.g., time spent feeding on biscuits/total time feeding), and the amount of food ingested (bite count/total time spent feeding on a particular food type). This study allowed the identification of native flora and fauna eaten by the lemurs, the time individuals spent eating provisioned food versus native flora, and how individuals varied in food type and food intake by age and sex. Non-parametric statistics were used and significance for all statistical tests was set at $P \leq .0.5$.

CHAPTER III

RESULTS

Sample Times and Totals

Over the course of my four month study, the five adult females and four juveniles were each sampled for eight rounds, for a total of 432 hours (one round = every focal animal sampled for three morning and three afternoon hours each). As a result of the late introduction of the new members, the adult males' sample times were much fewer than the rest of the group's (Nick: 12 morning hours and 12 afternoon hours; Pan: 9 hours; rest of group: 48 hours/individual). Pan was sampled for only 9 hours (3 morning hours and 6 afternoon hours) because he died on November 13, 2006. Including the adult males, I sampled the group for a total of 465 hours.

Time Spent Feeding and Time of Day

A significant relationship was found between time spent feeding and time of day (Kruskal-Wallis, DF = 5, H = 32.073, P = <.0001). Lemurs ate more food (provisioned and natural) during the second and third afternoon hours than any other time of day (range from 15:00 to 19:36). When the lemurs foraged in the afternoon, they spent significantly more time feeding on hard to digest/low quality foods (bark, galls, leaves, seeds, stems, and twigs) than easy to digest/high quality foods (fruits and flowers; Spearman Rank, Z-value = 9.472, P = <.0001).

Identified Species and Parts of Plants

In addition to a daily provisioned diet of primate chow and fruits (apple, banana, blueberry, fig, grape, pear, and sweet potato) lemurs consumed a total of 30 different species of natural foods during the study period, which were identified whenever possible (Table 3.1). Natural foods consumed that were not identified include bark lice web, grass, lichen, and soil. No insects or other native fauna were observed to be consumed by any individuals during sampling, even though on a few occasions, I casually observed resting individuals to bite at a mosquito or fly buzzing about. In addition, I observed two different individuals burrowing their heads inside a tree trunk hole for at least the allotted time of a feeding bout (> 10 seconds). My assumption was that they were extracting insects or drinking rain water, but I could not be certain of their activity, so I did not include these possible feeding bouts in my data set.

Table 3.1: List of Native Flora

Scientific Name	**Common Name**
Acer rubrum	Red maple
Bumelia tenax	Tough bumelia
Diospyros virginiana	Common persimmon
Helianthemum corymbosum	Frost weed
Ilex opaca	American holly
Liquidambar styraciflua	Sweetgum
Lyonia ligustrina	Maleberry
Magnolia grandiflora	Southern magnolia
Mikania scandens	Climbing hempweed
Myrica cerifera	Wax myrtle
Nyssa sylvatica	Blackgum
Persea borbonia	Red bay
Phoradendron flavescens	American mistletoe
Pinus echinata	Shortleaf pine
Pinus palustris	Longleaf pine
Pinus taeda	Loblolly pine

Table 3.1-Continued: List of Native Flora

Pleopeltis polypodioides	Resurrection fern
Pterocaulon pycnostachyum	Black-root
Quercus alba	White oak
Quercus laurifolia	Laurel oak
Quercus nigra	Water oak
Quercus virginiana	Live oak
Sabal palmetto	Cabbage palm
Saururus cernuus	Lizard's tail
Smilax auriculata	Greenbrier
Smilax laurifolia	Bamboo vine
Tillandsia usneoides	Spanish moss
Toxicodendron radicans	Poison oak
Vaccinium arboreum	Sparkleberry
Vitis rotundifolia	Muscadine

Of the various parts of plants, I observed the lemurs to only forage on bark, flowers, fruits, galls, leaves, seeds, stems, and twigs. The phenophase of plants include the following: new, mature, and dead leaves, ripe and unripe fruits, new bark, dead bark, and dead stems. There was one instance when a focal animal stripped the bark off a pine tree sapling. I included this activity into my data set as a feeding bout and categorized the phenophase of the bark as "new." At times, I was unable to identify parts of plants and the phenophase of parts due to lack of visibility or certainty. In such cases, the unknown parts and/or phenophase were denoted as "N/A" in the data set.

Comparison of Natural Plants Eaten With Other Studies

Of these 18 plants species recorded by Keith-Lucas et al. (1999), I observed the lemurs in my study to forage on eight of those species (Table 3.2; Appendix A). Dierenfeld and McCann (1999) reported that the lemurs to consumed 30 different species of plants and 15 of those species are represented in my study (Table 3.2; Appendix A).

When the lemurs ate natural foods in Savage's (2005) study, they fed upon 24 different species, 18 of which are represented in my study (Table 3.2; Appendix 1). However, nine species of plants that the lemurs foraged on in my study were not previously recorded (*Helianthemum corymbosum*, *Liquidambar styraciflua*, *Lyonia ligustrina*, *Mikania scandens*, *Nyssa sylvatica*, *Pinus echinata*, *Quercus alba*, *Saururus cernuus*, and *Smilax auriculata*; Appendix A).

Table 3.2 Natural Plants Eaten by *L. catta* on St. Catherines Island

Acer rubrum	Savage, 2005
Bumelia tenax	Dierenfeld & McCann, 1999
Diospyros virginiana	Dierenfeld & McCann, 1999
Ilex opaca	Dierenfeld & McCann, 1999; Savage, 2005
Magnolia grandiflora	Dierenfeld & McCann, 1999; Keith-Lucas et al., 1999; Savage, 2005
Myrica cerifera	Dierenfeld & McCann, 1999; Keith-Lucas et al., 1999; Savage, 2005
Persea borbonia	Dierenfeld & McCann, 1999; Keith-Lucas et al., 1999; Savage, 2005
Phoradendron flavescens	Dierenfeld & McCann, 1999
Pinus palustris	Savage, 2005
Pinus taeda	Dierenfeld & McCann, 1999; Keith-Lucas et al., 1999; Savage, 2005
Pleopeltis polypodioides	Dierenfeld & McCann, 1999; Savage, 2005
Pterocaulon pycnostachyum	Savage, 2005
Quercus laurifolia	Savage, 2005
Quercus nigra	Savage, 2005
Quercus virginiana	Dierenfeld & McCann, 1999; Keith-Lucas et al., 1999; Savage, 2005
Sabal palmetto	Dierenfeld & McCann, 1999; Keith-Lucas et al., 1999; Savage, 2005
Smilax laurifolia	Dierenfeld & McCann, 1999
Tillandsia usneoides	Dierenfeld & McCann, 1999; Savage, 2005
Toxicodendron radicans	Savage, 2005
Vaccinium arboreum	Dierenfeld & McCann, 1999; Keith-Lucas et al., 1999; Savage, 2005
Vitis rotundifolia	Dierenfeld & McCann, 1999; Keith-Lucas et al., 1999; Savage, 2005

Natural Versus Provisioned Feeding Percentages and Rates

Out of the 465 total hours in which I observed the lemurs, feeding occurred only 11.1% of the time (time spent feeding/total time observed). During feeding bouts, lemurs spent the majority of their time foraging between 0-5 meters (Figure 3.1). While overall feeding time is low as compared to total time observed, there is a highly significant difference between natural feeding and provisioned feeding rates (Mann-Whitney U, Z-value = -14.362, P = <.0001). Overall, the lemurs spent 58.2% of their feeding time consuming natural foods. As for the amount of food ingested (bite count/total time spent feeding on a particular food type), there is a highly significant difference between natural feeding and provisioned feeding rates (Mann-Whitney U, Z-value = -10.004, P = <.0001). Overall, when bite counts were visible, the lemurs consumed a greater amount of natural foods than provisioned foods.

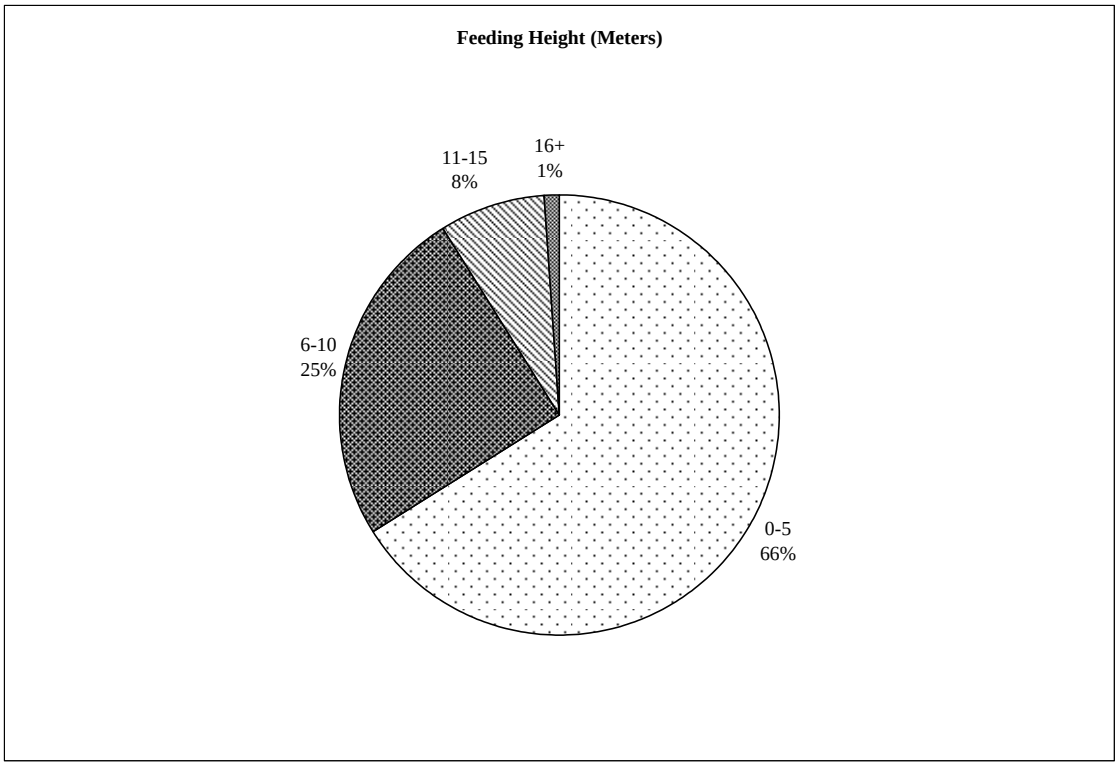

Figure 3.1: Time Spent Feeding at Varying Height Levels

In addition, when lemurs fed on natural foods, they spent most of their time feeding on *Sabal palmetto* and species of the genus *Quercus*: *Q. alba, Q. laurifolia, Q. nigra,* and *Q. virginiana* (Kruskal-Wallis, DF = 27, H = 203.055, P = <.0001; Figure 3.2). As for the part of a plant, lemurs spent more time feeding and consumed a greater amount (bite count/total time spent feeding on a particular food part) of fruits than other parts of plants (Kruskal-Wallis, DF = 7, H = 123.711, P = <.0001; Kruskal-Wallis, DF = 7, H = 59.966, P = <.0001; Figure 3.3). Overall, lemurs spent 58.0% of their feeding time on native resources consuming fruits. The lemurs ate fruit from nine different genera but concentrated heavily on the fruit of *Sabal palmetto* (Figure 3.4).

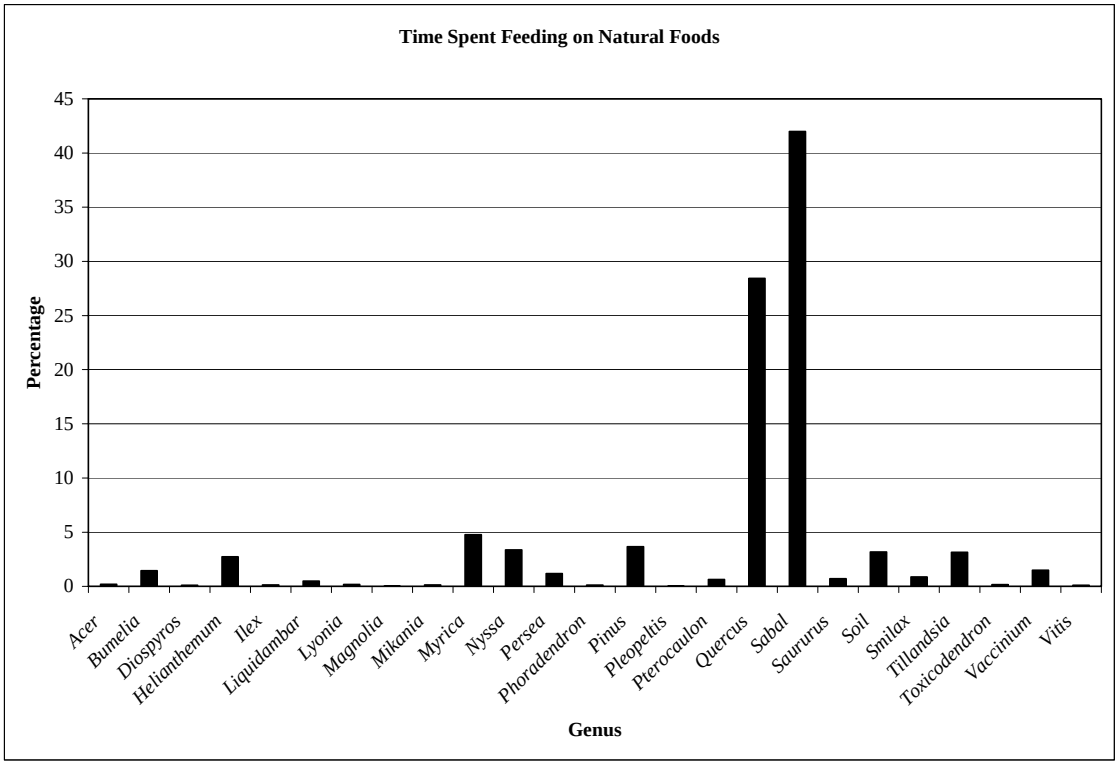

Figure 3.2: Degree of Natural Food Preference (Genus)

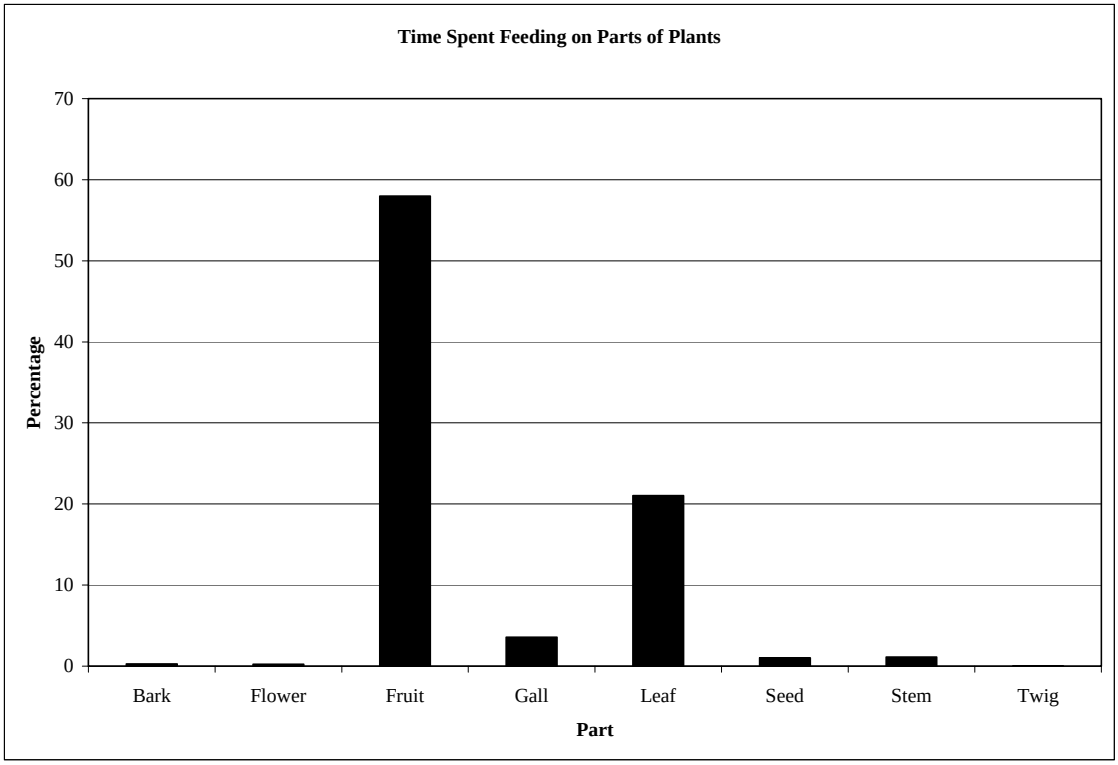

Figure 3.3: Degree of Preference (Part of Plant)

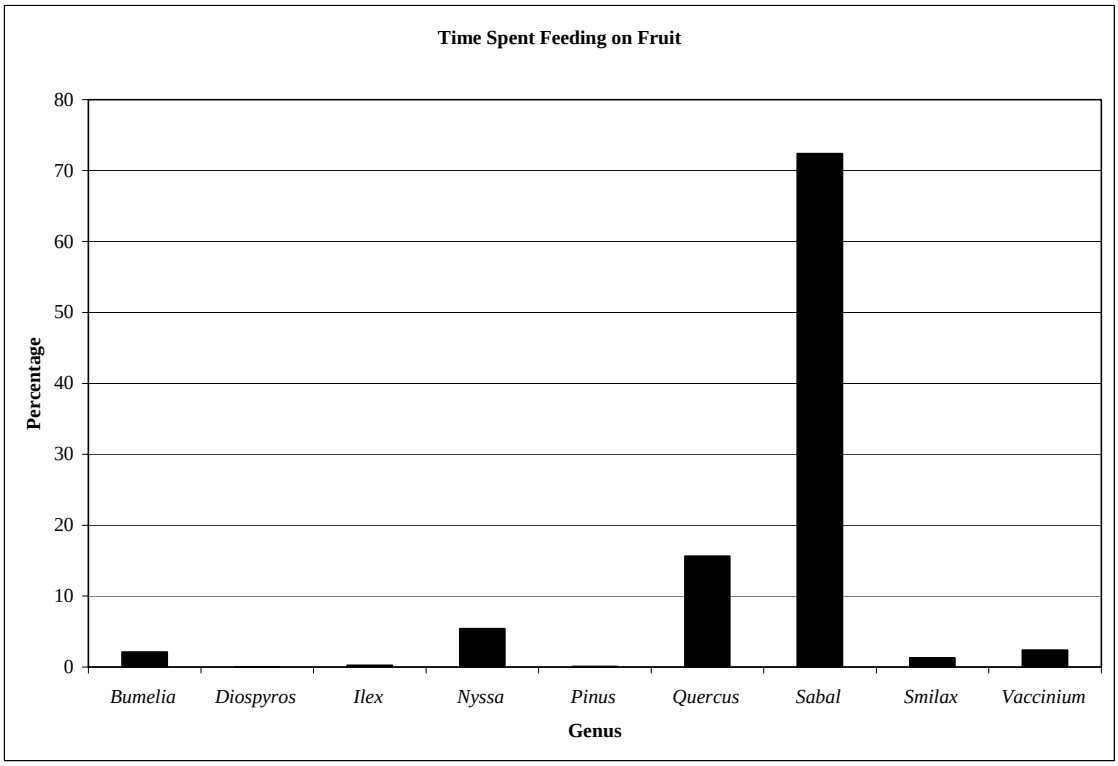

Figure 3.4: Degree of Preference on Genus (Fruit)

Although the lemurs spent less of the feeding time on natural resources consuming leaves (21.0%; Figure 3.3), they fed on leaves from 21 different genera, concentrating on *Helianthemum*, *Myrica*, *Pinus*, *Quercus*, and *Tillandsia* (Figure 3.5). It is also interesting to note that when lemurs foraged upon galls and seeds, they concentrated on only one genus (*Quercus* and *Pinus*, respectively). There was only one instance in which a lemur fed upon a twig, and it was from *Quercus virginiana*. Degree of genus preference was also accounted for bark (*Persea*, Figure 3.6), flower (*Phoradendron*, Figure 3.7), and stem (*Pterocaulon* and *Saururus*, Figure 3.8).

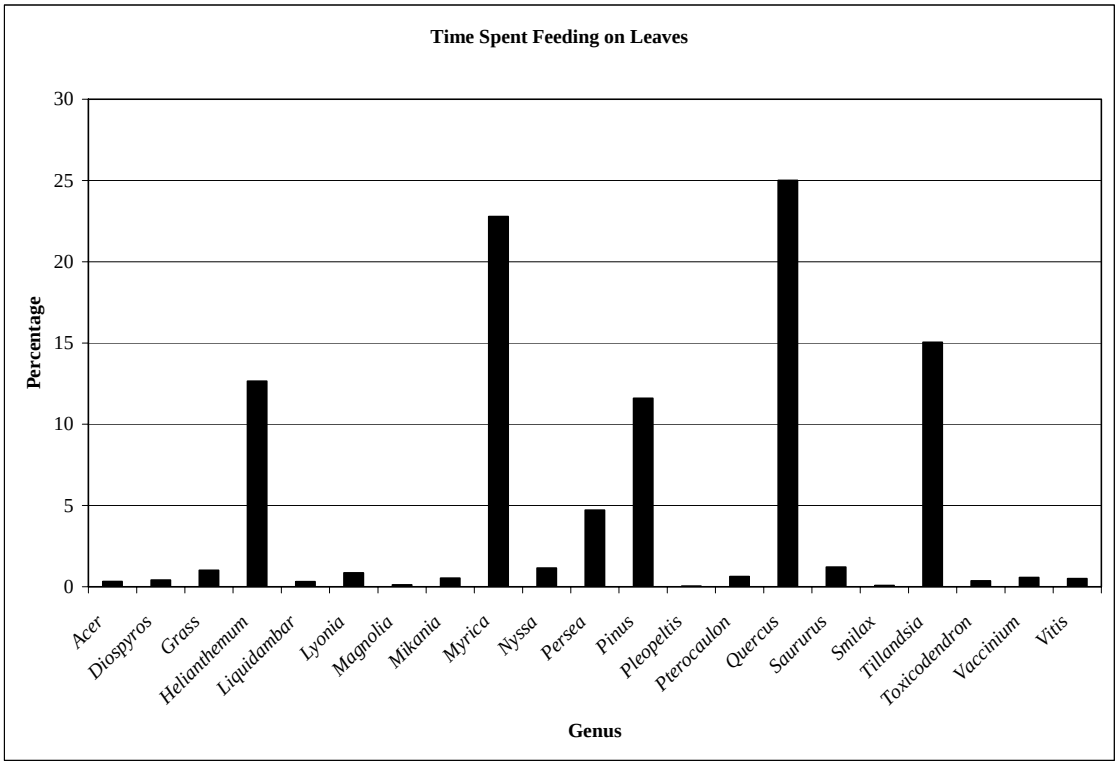

Figure 3.5: Degree of Preference on Genus (Leaves)

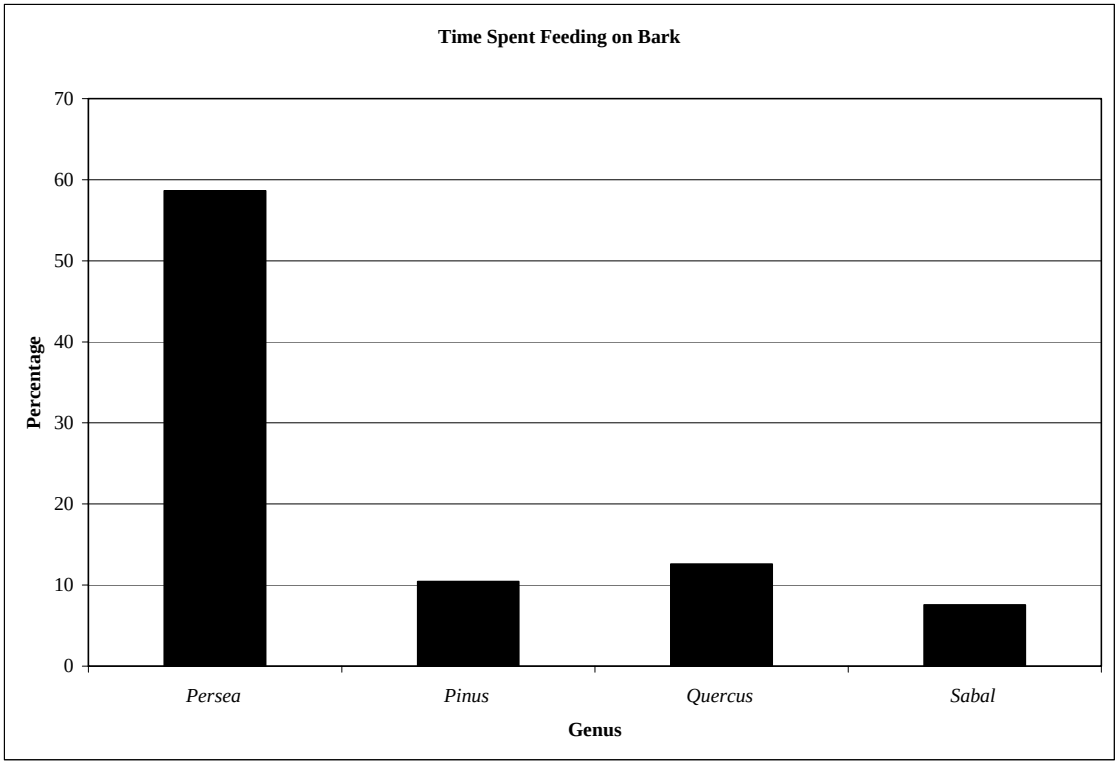

Figure 3.6: Degree of Preference on Genus (Bark)

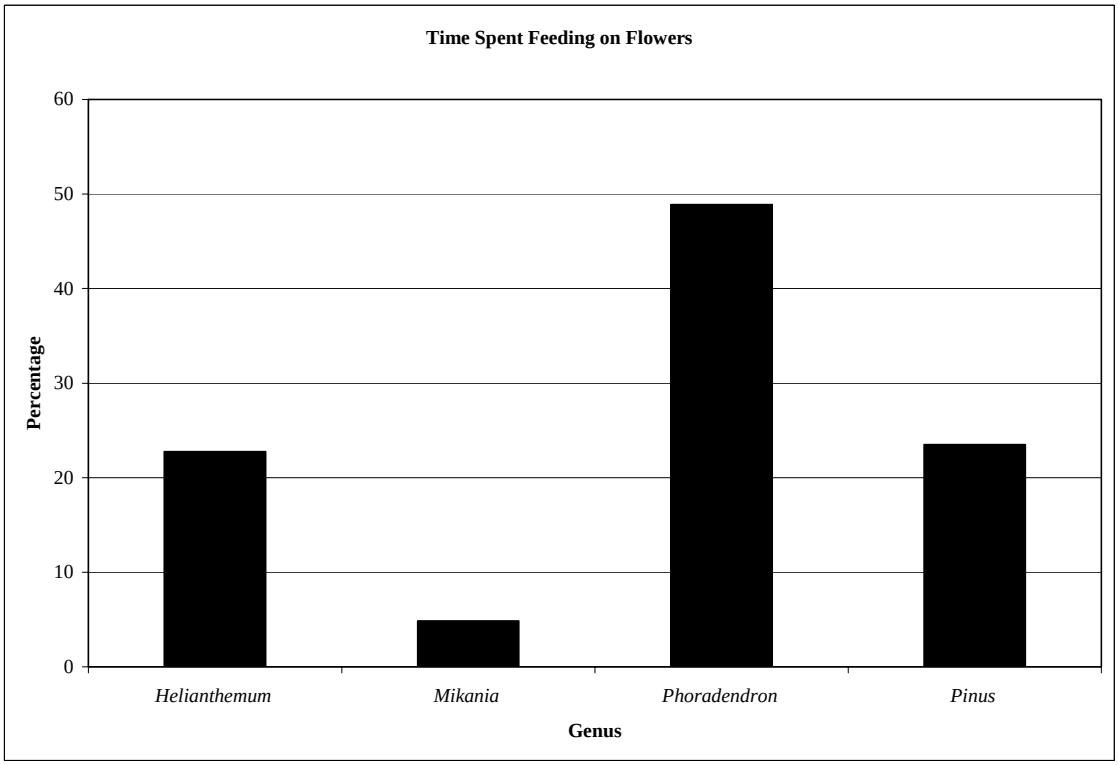

Figure 3.7: Degree of Preference on Genus (Flowers)

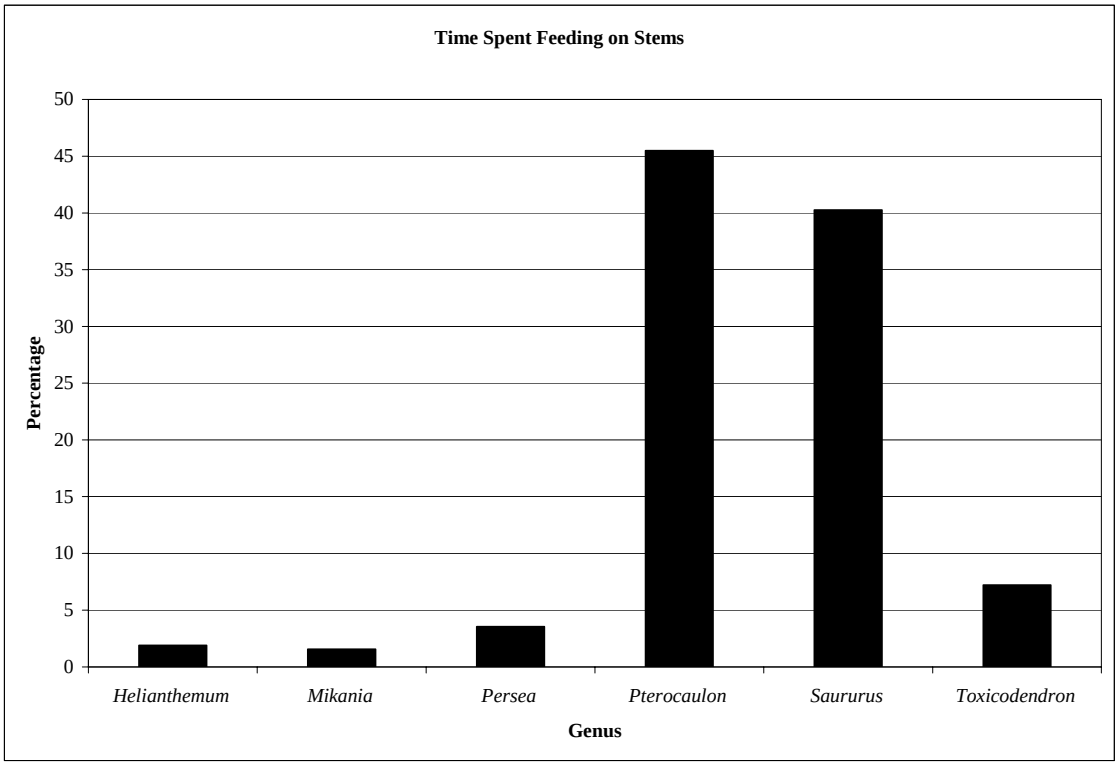

Figure 3.8: Degree of Preference on Genus (Stems)

Lastly, as it was occasionally difficult to ascertain the part of plant that was being consumed (16.9% of natural feeding time was denoted as "N/A" for part of plant), I was unable to identify the phenophase of the part of plant due to limited sight or lack of proper classification (e.g., bark, gall, seed). In fact, 40.5% of the time lemurs spent feeding on natural foods, I was unable to determine the phenophase. However, when I identified the phenophase of the part of plant, lemurs spent most of their natural feeding time foraging upon ripe fruit (Table 3.3). In addition, when taking individual parts of plants into account, lemurs also foraged upon dead bark and stems, and ripe fruit (Table 3.4). As for the phenophase of leaves, the majority of leaf feeding bouts (55.4%) was of an unknown status and at heights of at least five meters.

Table 3.3: Time Spent Feeding on Natural Foods (Phenophase)

N/A	bark, flower, gall, seed, stem, twig, or limited sight	40.5%
Ripe	fruit	31.6%
Both (unripe & ripe fruit or new & mature leaves)	fruit, leaf	9.9%
Unripe	fruit	8.9%
Mature	leaf, bark	6.5%
Dead	leaf, bark, stem	1.4%
New	leaf, bark	1.2%

Table 3.4: Time Spent Feeding on Part of Plant (Phenophase)

Bark	**Dead**	**57.2%**
	N/A	36.3%
	New	6.5%
Fruit	**Ripe**	**54.4%**
	N/A	20.1%
	Unripe	15.3%
	Both	10.1%
Leaf	**N/A**	**41.4%**
	Mature	31.1%
	Both	19.2%
	New	5.8%
	Dead	2.5%
Stem	**Dead**	**63.1%**
	N/A	37.0%

Age, Sex, and Focal Differences

No significant difference was found in time spent feeding by age group (adult versus juvenile) (Mann-Whitney U, Z-value = -1.089, P = .2760). When comparing adult and juvenile females only (due to the greater number of individuals and even number of sample times), no significant difference was found between time spent feeding and age

group (Mann-Whitney U, Z-value = -.130, P = .8963), or between amount of food ingested and age group (Mann-Whitney U, Z-value = -.233, P = .8157).

Even though I sampled females to a much greater extent than males, no significant difference was found between time spent feeding and sex (Mann-Whitney U, Z-value = -.669, P = .5036). In addition, no significant difference was found between amount of food ingested and sex (Mann-Whitney U, Z-value = -1.540, P = .1236).

Lastly, I focused upon five adult females (Becky, Holly, Rachel, Jen, Marie) in an attempt to address individual differences in time spent feeding or amount of food ingested as a possible result of age or dominance rank. No significant difference was found in the amount of food ingested (Kruskal-Wallis, DF = 4, H = 8.789, P = .0666), but significant individual differences were found in time spent feeding (Kruskal-Wallis, DF = 4, H = 10.833, P = .0285). A significant correlation was found between age and time spent feeding (Spearman Rank, Z-value = 2.402, P = .0163). Marie (12 years old) spent the most time feeding compared to the other females, but Jen (8 years) and Becky (2 years) spent approximately the same amount of time feeding as Marie. Holly (3 years) spent significantly less time feeding than those three females and Rachel (5 years) spent significantly less time feeding than Holly. Therefore, the oldest adult female individual spent significantly more time feeding than the middle-aged (Rachel and Jen) and young adult females (Becky and Holly).

In sum, no significant differences or correlations were found except when comparing natural and provisioned feeding rates, time of day and time spent feeding, and dietary differences between adult females. Lemurs preferred feeding on natural foods

(particularly upon the fruits of *Sabal palmetto* and the acorns and leaves of *Quercus* spp.) during late afternoon hours from heights of 0-5 meters.

CHAPTER IV

DISCUSSION

The main objective of my study was to identify the natural plant resources foraged by the ringtailed lemurs on St. Catherines Island (SCI). Previous studies on SCI, all of which have covered a span of one year, have reported natural foods consumed by the lemurs (Keith-Lucas et al., 1999; Dierenfeld and McCann, 1999; Savage, 2005). While my study was only conducted over a period of four months (late August to mid December), it is important to compare the plant resources I identified with those identified by Keith-Lucas et al. (1999), Dierenfeld and McCann (1999), and Savage (2005) in order to note any changes in the lemurs' diet.

Plant Species Consumed by Lemur catta on SCI

There was a great deal of overlap between the natural plants foods the ringtailed lemurs foraged on in this study and other studies. I found a 44% overlap in the natural foods eaten by the lemurs with a study conducted by Keith-Lucas et al. (1999). Their study covered a span of seven years following the first release of ringtailed lemurs onto SCI and Keith-Lucas et al. (1999) observed the social and ecological behaviors of the lemurs. In another study, Dierenfeld and McCann (1999) collected data on the natural feeding bouts of the ringtailed lemurs at SCI at quarterly intervals (February, May,

August, November). Of 30 different plant species Dierenfeld and McCann (1999) reported the lemurs to consume, 15 of those species were eaten by the lemurs during my study. Finally, there was a 75% overlap in the natural plant foods the lemurs ate in my study compared to Savage (2005). However, I found lemurs to forage on nine previously unrecorded plant species on the island. This may be largely due to the greater number of observation hours I conducted on feeding bouts, which increased the chance of observing foraging bouts on native species. Thus, when all four studies are considered, the lemurs could potentially forage on at least 53 different plant species because none of these studies were done continuously over the course of a year. Another possible reason for the high number of previously unrecorded forages is differences in plant distribution at the feeding sites and within home ranges of the three groups of lemurs. For example, during my initial visit to the island, I observed lemur Group 1 to forage on berries from *Melia azedarach*. This particular species is very limited in its distribution on the island and I have only seen it in one location, which is closest to Group 1's feeding site. I did not observe my study group, Group 3, to forage on *Melia azedarach* or to travel to its location. Therefore, each lemur group may eat approximately the same number of plant species but differ in the variety of forages they consume due to plant distribution; although Savage (2005) did not observe any significant natural dietary differences between her four study groups on the island.

Provisioned and Foraging Rates

In addition to recording the number of different plant species foraged, feeding bouts were calculated to examine the differences between provisioned and foraging rates. Out of the total time observed, Savage (2005) and Dierenfeld and McCann (1999) found

that feeding took up approximately 20% of the lemurs' activity budget, whereas I found that the lemurs only fed 11.1% of the total time observed. My study and Savage's study included both provisioned and natural feeding rates and Dierenfeld and McCann's study included only natural feeding rates. The time that lemurs spent feeding in my study corresponds to the time that the ringtailed lemurs in Ganzhorn's (1986) DUPC study spent feeding (about 12%) as compared to the rest of their activities. However, Ganzhorn's (1986) feeding rate does not include provisioned feeding. No percentage in relation to total time spent feeding and total time observed was reported by Keith-Lucas et al. (1999). Keith-Lucas et al. did provide provisioned and foraging rates and found that their focal animals heavily relied upon provisioned foods since they were adjusting to a free-ranging environment from a captive one. In fact, provisions comprised 83.0% by mass of the animals' diet. However, once foraging percentages were corrected for season, the rate of foraging did not increase in the following seven years of the lemurs' release. On the other hand, Savage (2005) found that the animals spent about half their feeding time on natural foods and half consuming provisioned foods. I calculated an even higher rate of time spent foraging (58.2%) compared with time spent eating provisions (41.8%). However, the higher rate of time spent foraging (58.2%) and the low overall feeding rate (11.1%) are partially due to the interruptions by visitors to SCI that occurred during the M2 and M3 hours of my data collection. These interruptions lasted an average of approximately 14 minutes and occurred on 19 separate focal samples which coincided with provisioned feeding. Therefore, approximately 266 total minutes (< 1% of total time observed) could have included many more provisioned feeding bouts. Additionally, 14 separate focal samples (M3 hour) ended before the staff primatologists

arrived to the feeding site to provision the group. If my focal animals did eat their provisions for the total 266 minutes, the differences in provisioned and foraging rates would have more closely reflected those reported by Savage (2005).

One final item in regards to the lemurs' foraging rate on the island includes the difference in the time spent feeding on low quality and high quality forages. A significant correlation was found between time spent feeding on low quality/high fiber foods (bark, galls, leaves, seeds, stems, twigs) and afternoon sample hours. My study group spent significantly more time feeding on hard to digest plant species in the afternoon than in the morning. This correlation may simply be a result of the lemurs being provisioned daily with high quality and high sugar fruits in the late morning. Therefore, the lemurs do not need to expend more energy and time foraging for patchily distributed high quality fruits and flowers, which were not readily and seasonally available during my study (with the exception of *Sabal palmetto* and *Quercus* spp.). Mowry and Campbell (2001) stated that, in general, the lemurs on SCI did not appear to select forages based on sugar or protein content. In addition, Mowry et al. (1997) found that the lemurs did not appear to avoid plant items high in secondary compounds and Dierenfeld and McCann (1999) found that the fiber values of the lemurs' natural diet were nearly 40%. Another reason why the lemurs spent more time feeding on lower quality foods in the afternoon may be correlated to the lemurs' activity level. The lemurs' emphasis on high fiber items preceded and coincided with sunset, just before the group should settle down for the night, which would allow for more time to process the hard to digest foods.

Degree of Preference in Plants

When the lemurs consumed natural plant items, only a few different species comprised the majority of their natural diet. During the first six weeks after the first group's release in 1985, the group foraged almost exclusively on *Vitis rotundifolia* and *Persea borbonia* leaves (97%; Keith-Lucas et al., 1999). The lemur group in Dierenfeld and McCann's (1999) study was observed to forage primarily on *Persea borbonia*, *Melia azedarach*, *Celtis laevigata*, *Celtis occidentalis*, *Sabal palmetto*, and *Juniperus virginiana*, although, no percentages were given. In Savage's (2005) study, lemurs preferred the buds and leaves of *Quercus* spp. (28%), the acorns of *Quercus* spp. (10%), the berries, stalks, and bark of *Sabal palmetto* (12-13%), and the leaves, fruit, and buds of *Vitis rotundifolia* (8-9%). During the months of my data collection, it is not surprising that lemurs spent most of their natural feeding time on *Sabal palmetto* (42.0%) and *Quercus* spp. (28.4%) since the fruits of these species are available during the late summer and fall. All other species in my study comprised less than 5% (per species) of the lemurs' natural diet.

Sex and Age-Related Dietary Differences

After the captive-born adult males, Nick and Pan, were allowed to free-range with the rest of the group, I did not expect them to transition as well as they did in their foraging skills. I expected the adult males to rely more heavily on their provisions since the plant items were unfamiliar to them. However, the males were able to adjust quickly to foraging. As Keith-Lucas et al. (1999) observed in their study, the individuals from the original SCI group began foraging even before their release. Prior to their release, this group was housed together in an enclosure at their potential release site for 10 weeks.

Next to the enclosure, *Vitis rotundifolia* and *Persea borbonia* were close enough for the lemurs to reach out through the cage wire and eat leaves from both plants. After the original group's release, group members continued to feed almost exclusively on those two plant species, whereas in my study Nick and Pan ate all of the items foraged on by the rest of their group. This difference may be due to the fact that all of the members of the original group were born and lived in captivity until their release on SCI (Keith-Lucas et al., 1999), while Nick and Pan joined a group of experienced individuals and, therefore, had many opportunities to learn which native plants foods to eat. During my focal samples on Nick and Pan, I never observed them to test a plant item and reject it, as was the case with the original group of released lemurs (Keith-Lucas et al., 1999). It is interesting to note that out of the six different species that the lemurs from the original group tested and rejected (Keith-Lucas et al., 1999), three of those species were eaten by the lemurs in my study: *Tillandsia usneoides* leaves, *Smilax laurifolia* fruit, and *Quercus virginiana* leaves.

Unexpectedly, I did not find any significant dietary differences between males and females. On several occasions, I casually observed the adult males to wait to feed on provisions or forages until the females finished feeding and moved away from the feeding enclosure or to other trees. According to Sauther's (1993) research on resource competition in populations of *Lemur catta* at Beza Mahafaly, males seemed to be under constant feeding stress throughout the year. In particular, Sauther (1993) observed that males had lost weight and appeared nutritionally stressed after the mating period because the males apparently fed less and physically exerted themselves more during the mating period. However, I consider the absence of dietary differences between males and

females in my study is largely due to the significantly fewer focal samples conducted on the adult males. It is possible that too few data were available to sufficiently compare feeding rates between the sexes.

Conversely, I sampled each adult female (Becky, Holly, Jen, Marie, Rachel) for the same number of hours (48 hours per individual) and a significant difference was shown to exist between the five adult females and the time spent feeding on natural and provisioned foods. Marie spent the most time feeding compared to the other females, but Jen and Becky spent approximately the same amount of time feeding as Marie. Holly spent significantly less time feeding than those three females and Rachel spent significantly less time feeding than Holly.

The SCI staff primatologists informed me of the background histories on several of the adult females; most notably, that Marie, the oldest female (12 years), was the dominant female in her group until her 8 year old daughter, Jen, replaced her as the top-ranking female. At the time of my study, Jen had the most offspring: three adult females, one juvenile female, one juvenile male, and one female infant. Jen's youngest adult daughter, Becky, was 2 years old and did not have any offspring. Therefore, due to the inconsistent ranking order of dominance and number of offspring females had, these reasons did not appear to be correlated with adult female dietary differences. However, when the females' ages were taken into account, a significant correlation was found between old age (> 10 years) and a higher rate of feeding, but age and time spent feeding did not follow a descending pattern. For example, if the correlation was consistent between age and time spent feeding, the order would have been as follows: Marie, Jen,

Rachel, Holly, Becky. Therefore, I do not consider age to be a reliable correlate of adult female dietary differences.

CHAPTER V

CONCLUSION

From the three previous studies that I have discussed (Keith-Lucas et al., 1999; Dierenfeld and McCann, 1999; Savage, 2005), my study shows the greatest number of plant species consumed by the ringtailed lemurs on SCI. Dierenfeld and McCann (1999) also observed the lemurs to forage on 30 different plant resources, but it is important to distinguish that their study covered a span of one year, whereas my study was only conducted during the late summer and fall. Therefore, the number of total forages that comprise the lemurs' diet could be significantly higher than expected for a provisioned population.

In addition to the relatively high number of plant resources foraged by the lemurs, there was a significant difference between provisioned feeding and natural feeding rates. The lemurs in my study spent the majority of their feeding time (58.2%) foraging on natural items, with an emphasis on *Sabal palmetto* and *Quercus* spp., which comprised 70.4% of their natural diet. In particular, the lemurs preferred to forage on the fruits of *Sabal palmetto* (42.0% of natural feeding time) and the acorns and leaves of *Quercus* spp. (14.4%).

I also examined dietary differences between males and females, juveniles and adults, and adult female individuals. With the exception of dietary differences between

adult females, no significant differences were found in relation to time spent feeding or amount of food ingested. I found no correlation between the time individual adult females spent feeding and dominance rank or number of offspring females had. While a significant correlation was found between old age and a higher rate of feeding, the correlation did not follow a consistent descending order. With these correlations excluded, differences in diet between adult females remain unclear at present.

Overall, my study serves as a beginning to a detailed investigation of the feeding behavior of *Lemur catta* on SCI. However, certain aspects of my data collection could be improved upon for the benefit of future feeding ecology research on SCI. First, while I conducted numerous focal samples, I only sampled one group and the adult males in my study were not nearly represented enough when compared to the females. This particular limitation was out of my control due to the late introduction of the captive-born males to my study group and the death of one adult male. Second, regular and continuous focal samples that coincide with provisioned feeding and are not interrupted are needed in order to determine more accurate comparisons of provisioned feeding rates. Third, too many feeding bouts were denoted as "N/A" due to my inability to clearly identify the part of plant (16.9% of natural feeding bouts) and the phenophase of the part of plant (40.5% of natural feeding bouts). Lastly, the data that I collected were limited to feeding rates over just one season out of the year.

Future research on the feeding ecology of ringtailed lemurs on SCI could expand to a much greater extent. For example, an examination could be conducted on the relationships between feeding rates of all three groups, other activities (e.g., traveling, resting, grooming, etc.), seasonal availability of forages, home range size and use of

home range. Savage (2005) investigated relationships between home range size, activity budgets, and provisioned and feeding rates, but it would be valuable to replicate these aspects of her study because too few observation hours (360 hours) were conducted over the span of one year. In addition, Mowry et al. (1997) and Dierenfeld and McCann (1999) collaborated and implemented the first nutrient composition study on the 30 plant resources consumed by the lemurs in their study, and it would be beneficial to continue additional nutritional and secondary compound analyses on untested forages. It would also be useful to collect and test fecal samples in order to determine any unknown forages consumed by the lemurs. Information resulting from these studies may help to set guidelines for the selection of release locations of lemurs on the island, as new groups can be introduced to areas where the same preferred items are abundantly located. Other research on feeding behavior could include an investigation into the differences in feeding rates among adult females during gestation, lactation, and weaning periods. Additionally, it would be interesting to calculate differences in agonistic rates (e.g., cuffing, biting, etc.) during provisioned and natural feeding bouts. Data on these research implications would be useful to the island's newly developed feeding ecology database, which serves as a resource to future researchers focusing on the behavioral ecology of *Lemur catta* on SCI.

APPENDIX A

Combined Plant List For All SCI Feeding Ecology Studies

Acer rubrum	Savage, 2005
Arundinaria gigantean	Dierenfeld and McCann, 1999
Bumelia tenax	Dierenfeld and McCann, 1999
Carya glabra	Keith-Lucas et al., 1999
Carya ovalis	Dierenfeld and McCann, 1999
Celits laevigata	Dierenfeld and McCann, 1999
Celtis occidentalis	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
Chaenomeles spp.	Keith-Lucas et al., 1999
Chenopodium ambrosiodes	Dierenfeld and McCann, 1999
Cornus florida	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
Diospyros virginiana	Dierenfeld and McCann, 1999
Ficus spp.	Keith-Lucas et al., 1999
Helianthemum corymbosum	
Ilex opaca	Dierenfeld and McCann, 1999
	Savage, 2005
*Ilex vomitoria**	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
Juniperus virginiana	Dierenfeld and McCann, 1999
Liquidambar styraciflua	
Lyonia ligustrina	
Magnolia grandiflora	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
	Savage, 2005
Melia azedarach	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
	Savage, 2005
Mikania scandens	
Morus alba	Keith-Lucas et al., 1999

Appendix-Continued

Morus rubra	Keith-Lucas et al., 1999
Myrica cerifera	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
	Savage, 2005
Nyssa sylvatica	
Parthenocissus quinquefolia	Dierenfeld and McCann, 1999
Persea borbonia	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
	Savage, 2005
Phoradendron flavescens	Dierenfeld and McCann, 1999
Pinus echinata	
Pinus elliottii	Keith-Lucas et al., 1999
	Savage, 2005
Pinus palustris	Savage, 2005
Pinus taeda	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
	Savage, 2005
Pleopeltis polypodioides	Dierenfeld and McCann, 1999
	Savage, 2005
Prunus caroliniana	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
	Savage, 2005
Pterocaulon pycnostachyum	Savage, 2005
Quercus alba	
Quercus laurifolia	Savage, 2005
Quercus nigra	Savage, 2005
Quercus virginiana	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
	Savage, 2005
Rubus betuifolius	Dierenfeld and McCann, 1999
Sabal palmetto	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
	Savage, 2005
Sassafras albidum	Savage, 2005
Saururus cernuus	
Serenoa repens	Savage, 2005

Appendix-Continued

Smilax auriculata	
Smilax laurifolia*	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
	Savage, 2005
Solanum nigrum	Dierenfeld and McCann, 1999
Tillandsia usneoides*	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
	Savage, 2005
Toxicodendron radicans	Savage, 2005
Vaccinium arboreum	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
	Savage, 2005
Vitis cinerea	Dierenfeld and McCann, 1999
Vitis rotundifolia	Dierenfeld and McCann, 1999
	Keith-Lucas et al., 1999
	Savage, 2005
Zanthoxylum clava-herculis	Dierenfeld and McCann, 1999
	Savage, 2005

Items in bold are included in my plant list. Items with an asterisk indicate plants that were tested and rejected by lemurs in the study by Keith-Lucas et al. (1999).

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