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Role of Provisions and Season on Foraging and Female Dominance Behavior in Ring-Tailed Lemurs (Lemur Catta) on St. Catherine's Island

Timothy Moore

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ROLE OF PROVISIONS AND SEASON ON FORAGING AND FEMALE
DOMINANCE BEHAVIOR IN RING-TAILED LEMURS (*LEMUR CATT*A) ON ST.
CATHERINE'S ISLAND

by

TIMOTHY MOORE

(Under the Direction of Michelle Cawthorn)

ABSTRACT

Madagascar is undergoing habitat destruction and degradation that is threatening its unique species, including ring-tailed lemurs. Ring-tailed lemurs (*Lemur catta*) live in matriarchal groups composed of a dominant female, adult males, subadult males and females, and young. Due to their dominance, it has been suggested that female ring-tailed lemurs have access to the highest quality resources and can monopolize food patches. Lemurs on St. Catherine's are free ranging and have unlimited access to natural food sources, but they are also provisioned with supplementary food to ensure a balanced diet. My study aimed to determine the impact of provisions on female dominance behavior and individual foraging behavior and whether or not this varied seasonally. During the summer of 2011, lemurs were presented with doubled amount of provisions; differences in foraging behavior and female dominance were determined. To assess the effect of season on foraging behavior and provision use, data collected in the summer (July-August 2011) were compared with winter (January 2012). Gender had no effect on type of food consumed naturally, but females spent more time at provision sites overall and during the first half of a provisioned feeding bout. Doubling of provisions resulted in equal time spent at provision sites for males and females, but no difference in activity pattern occurred. No difference was been found in food type consumed between genders,

but acorns seemed to be the favorite in both seasons. Lemurs were less active during the winter, and spent less time at provision sites. Overall, females are spending more time at provisioned food bowls than males suggesting females are consuming more. However, they are spending the same amount of time naturally foraging and foraging on the same types of natural food items. Overall, females seem to be eating more than males during the summer, indicating a possible increased need for sustenance by females possibly due to lactation. Season had an apparent effect on interest in provisions, on number of species consumed, and on activity type. My results provide valuable information to be used in future ring-tailed lemur translocations.

INDEX WORDS: Ring-tailed lemur, Female dominance, Foraging behavior, Provision use, Seasonality

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B.S., Auburn University, 2010

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CHAPTER 1

INTRODUCTION

According to the International Union for the Conservation of Nature (IUCN 2012), over 10,000 animal species are threatened with extinction. Of these, approximately 5,000 are considered vulnerable, 3,000 are considered endangered, and 2,000 are considered critically endangered. Over 700 modern species are extinct or extinct in the wild. Globally, extinction rates are as high 1000 times that of the background rate. This is due to increasing habitat destruction (which affects nearly 90% of all threatened species), pollution, and over exploitation (as well as other threats) (Baillie et al. 2004; IUCN 2007; Seddon et al. 2007; Wake and Vrendenburg 2008). Tropical forests have been especially hard hit. Estimates suggest that about half of the world's tropical forests have been lost (Skole and Tucker 1993).

A common tactic of animal conservation involves reintroduction of animals into native habitat, and understanding basic biology of species is critical to creating accurate and realistic species survival plans (AZA 2009). Reintroductions are a type of translocation, or “movement of living organisms from one area to another” (IUCN 1987). Other types of translocations are re-stocking and introducing species into non-native habitat (IUCN 1987). Reintroductions of representatives of diverse taxa have been attempted, including birds, mammals, fish, and invertebrates (Seddon et al. 2007). One review found that over 50% of reintroductions were mammals (Fischer and Lindenmayer 2000); another found 35% of 489 total reintroductions as of 2005 were mammals (Seddon et al. 2007). A notable success was the American bison *Bison bison*, one of the first reintroductions on record. Other successful introductions include the

Golden Lion Tamarin, *Leontopithecus rosalia*, Arabian oryx, *Oryx leucoryx*, and Przewalski's horse, *Equus ferus przewalskii* (Kleiman 1989; Stanley Price 1989; Van Dierendonck and Wallis de Vries 1996). Reviews of published reintroduction studies indicate that overall success rate is low, and wild-born animals have more success than captive born (Fisher and Lindenmayer 2000; Kleiman 1989).

Reintroductions are not simple and the process raises many questions including how much provisioning, if any, should be given to reintroduced animals and for how long (Fisher and Lindenmayer 2000; Armstrong and Seddon 2007). The addition of support in the initial phase of mammalian reintroductions in the form of medical care, shelter, or food appears to reduce rate of failure (Fischer and Lindenmayer 2000). This support is part of a "soft" release, in contrast to a "hard" release where animals receive no support. In a successful release of ruffed lemurs, *Varecia variegata variegata*, food was provided after release and their health and behavior were monitored (Britt et al. 2004). There have been many calls and attempts in recent years to establish guidelines before and after the reintroduction in order to refine the process, advance the field, and increase successes (Armstrong and Seddon 2007; Fischer and Lindenmayer 2000; Kleiman 1989; Seddon et al. 2007). Considering the overall expense of reintroduction projects, which can range from hundreds of thousands to millions of dollars (Kleiman 1989), it is critical to understand this relationship and the biology of the species in question both for the animals' health and for economic reasons.

For some species, reintroduction into the original native range may be impossible due to habitat loss. Madagascar is an excellent example of an area with significant habitat loss (Gade 1996) for which successful reintroductions of threatened or endangered species appear unlikely. Only ~7% of primary forest area remains in Madagascar, and tree cover of any kind has been

reduced to ~15% by activities like wood cutting and burning. Consequently, the entire biota of the island is threatened with extinction with over 800 species listed as threatened (Gade 1996; IUCN 2012). The IUCN has recently proclaimed the mammals of Madagascar to be the most threatened in the world (Yoder and Welch 2012). Due to this threat, attempts are in progress to preserve the forest and the species that depend on it (McConnell and Sweeney 2005).

An important component of the fauna of Madagascar is the group of primates known as lemurs. Lemurs live in many zoos around the world and a goal of many zoos is to return some of these species to the wilds of Madagascar (AZA 2009). The Madagascar Fauna Group worked in 1997 to successfully release black and white ruffed lemurs that had been bred in captivity back into Madagascar to restock a native population (Britt et al. 2004). Provisions are an important part of reintroductions for primates and captive animals (Fischer and Lindenmayer 2000; Konstant and Mittermeier 1982; Tear and Ables 1999), and were used in the Britt et al. (2004) study. Conservation efforts to preserve habitat, in conjunction with a soft release, suggest that it is a realistic possibility for lemurs to be reintroduced into their former ranges.

Another lemur species, the ring-tailed lemur, has been introduced to St. Catherine's Island, GA, (SCI) which provides an excellent opportunity to examine their behavior in an introduction setting. St. Catherine's Island is privately owned and managed by the St. Catherine's Island Foundation. Beginning in 1974, several endangered species of reptiles, birds, and mammals were located on the island due as a joint effort by the SCI foundation and the Wildlife Conservation Society (WCS) (Bell 2001; Wildlife Conservation Society 2012). The WCS ended their involvement with the program in 2003 (Bell 2001), but SCI continues to manage hornbills, hoofstock, and ring-tailed lemurs. The lemurs are semi-free ranging on the northern side of the island and exhibit species-typical behaviors (Keith-Lucas et al. 1999). This

population provides an opportunity to study and understand the challenges associated with introductions.

St. Catherine's Island differs from sites in Madagascar where lemurs remain such as Berenty and Beza Mahafaly in several ways. Climatic differences cause different seasons, and lead to completely different plant communities. Because the lemurs on SCI are living in non-native habitat and a different climate, they are provided food and water daily. Daily provisions include precise amounts of vegetables, fruits, and primate biscuits. Troop sizes on SCI range from five to over twenty individuals (Royce Hayes, pers. comm.), but there is a relative lack of range overlap in the SCI population (Keith-Lucas pers. comm.). Even though they are provisioned, *Lemur catta* also forage naturally on SCI (Keith-Lucas et al. 1999). By being provisioned, the importance of natural foraging in the SCI population may be reduced (Dierenfeld and McCann 1999). Fifty-three different natural species have been found in the diet including *Celtis* (mulberries), *Ficus* (figs), and *Melia azedarach*. However, seasonal differences in diet, activity, and provision use with respect to gender have yet to be quantified on SCI.

In the tourist areas in Berenty, lemurs have constant access to water and receive provisions (Jolly et al. 2002). However, the method of provisioning in this site is vastly different from SCI because tourists provide fruits at random (Jolly et al. 2002). Troop sizes range from three to over twenty individuals (Mittermeier et al. 1994), and their ranges overlap (Jolly 1972). On Berenty Reserve, there are at least 66 forage species of plants (Simmen et al. 2003). Similar to SCI, lemurs forage on *Ficus* and *Celtis* for figs and mulberries (different species), as well as the introduced species *Melia azedarach* (Simmen et al. 2003). This willingness to forage on introduced species (Jolly et al. 2002) suggests that they are flexible foragers. Overall, it is clear there are differences between SCI and Madagascar in most forage species, climate, and method

of provisioning but similarities in some forage species, troop sizes, and diversity in number of plant species in the diet.

Foraging on non-native species may pose risks to lemurs. Two studies on SCI have measured nutrients and secondary compounds in ring-tailed lemur diets (Mowry et al. 1997, Dierenfeld and McCann 1999). Mowry et al. (1997) measured condensed tannins, total phenols, and hydroxydiphenoglucose in different parts of plants (fruits, leaves, acorns, woody tissue, and other). Crude protein and fat, water-soluble carbohydrates, cell wall fiber, and minerals were measured in different parts of plants (leaves, buds, seeds, wood, and fruits) in Dierenfeld and McCann's study (1999). These studies found that the high fiber content of the plant diet on SCI is similar to that of wild populations. But lemurs on SCI eat less protein in their wild diet than their counterparts in Madagascar. This may be due to the fact that the primate biscuit provides an abundance of protein (Ganzhorn 1986; Dierenfeld and McCann 1999). Lemurs have been provisioned since their first release in 1985 (Keith-Lucas et al. 1999), well before Dierenfeld and McCann's study (1999), so they are not provisioned as a consequence of low protein. Their wild diet on SCI has also been found to be lacking in sodium, phosphorous and iron (Dierenfeld and McCann 1999), but provisioned primate biscuit may address this.

In both introductions and reintroductions, uncertainty remains regarding provisions (Fisher and Lindenmayer 2000; Armstrong and Seddon 2007). One question concerning provisions is whether they should be provided at all, and if so, in what quantity and for how long? The answers to these questions are complicated by species-specific behavior such as female dominance. Female ring-tailed lemurs are dominant to all males of the troop (Jolly 1966; Pereira et al. 1990), a rare occurrence among mammals. Another mammalian species that exhibits this form of dominance is the spotted hyena *Crocuta crocuta* (Frank 1986). In both

ring-tailed lemurs and spotted hyenas, groups have variable numbers of individuals, and females have feeding priority (Frank 1986; Mittermeier et al. 1994; Sussman 1992; White et al. 2007). Other examples of female dominance in mammals are found in the Columbian ground squirrel, *Spermophilus columbianus*, and bonobo, *Pan paniscus* (Murie and Harris 1988; White and Wood 2007).

Female ring-tailed lemurs have been found to have priority of access to food resources in both experimental (White et al. 2007) and natural (Pereira et al. 1990; Sauther et al. 1999) settings. They will control the food resource they are consuming against males, especially younger natal (offspring of females yet to disperse) males that rank lower in the dominance hierarchy; dominant males often defer to females (White et al. 2007). Differences in provisioned patch size might lead to differences in female behavior. For example, a small, provisioned patch (because of its size) might be considered a high-quality resource. If so, then females should use this resource vigorously, causing subordinate members of the troop to feed on lower quality food sources or not feed at all on some items. In White et al.'s (2007) experimental study, dominant females were able to control small patches (1-2-m radius), while in larger patches (4-m radius), less aggression was seen between the two sexes. However, dominant females consumed more food than males in all patch sizes.

Coleman (2007) and Savage (2005) looked at overall group foraging behavior on SCI and time spent consuming provisions and foraging. Savage's (2005) study examined whether provision use varied among troops and varied seasonally. The study did not address gender differences and only looked at provision use at the troop level. Savage found that the rate of consuming provisions and natural forage was roughly equal, but at the time (2005) provision amounts were higher than they are currently. Coleman's (2007) study compared feeding on

provisions and natural forage, examining which non-provisioned items were preferred and if gender affected feeding. However, male sample size and sample hours were low and thus it was difficult to identify any significant relationships of gender on foraging. She observed a few cases where, prior to feeding on provisions, a male waited on females to finish feeding before he fed. This seems to suggest a female feeding priority and leads to questions about female monopolization of provisions, how this affects other members of the troop, and who is next in line to feed on provisions. If females are monopolizing provisions, then males could be feeding on different natural plant parts or species to account for this deficiency. Coleman (2007) also found that all the lemurs in her study fed more on fruits when feeding naturally and that overall, they fed more on natural items than on provisions. However, she mentioned that human visitors on the island caused interruptions at the feeding stations that could have shortened or reduced time spent feeding on provisions.

Given that most plant species on SCI flower and bloom during the spring/summer (Coleman 2007), it seems winter would be a time of fewer available forage species and that females would dominate these resources. Savage's (2005) study did not test for gender differences across season in provisions. Coleman's (2007) study did not have a long enough sampling period to sufficiently compare males and females foraging and consumption of provisions. Examining the SCI lemurs for gender differences in foraging behavior will provide additional information to be used in future translocations. Additionally, there is a need to identify differences between the season patterns on SCI and Madagascar (SCI: cold/ warm seasons; Madagascar: rainy/dry).

Another question with introductions involves resource use. In an introduction, individuals are not in their historical native range with known natural food resources. The

availability of different forage species raises the question of whether or not these species are suitable for the introduced species. Given the change in forage species, generalists appear to be the most likely to succeed in introductions. However, the biology of the introduced species must also be taken into consideration.

Several studies have cataloged natural forage species on SCI (Dierenfeld and McCann 1999; Keith-Lucas et al. 1999; and Savage 2005); the most recent reported nine new species resulting in a total of 53 observed forage species (Coleman 2007). One of the forage species found to be important in all of the studies (Keith-Lucas et al. 1999; Dierenfeld and McCann 1999; Savage 2005; Coleman 2007), redbay (*Persea borbonia*), has been drastically affected by laurel wilt disease (Koch and Smith 2008) in the coastal Carolina and Savannah, GA area. Since its introduction, the disease has spread rapidly across the southeast to over sixty counties (Koch and Smith 2008). It is now found in Florida, Mississippi, Georgia, and both Carolinas (USDA 2012). It has been on St. Catherine's Island since at least 2003 (Cameron et al. 2008). The disease kills most redbay, so they are no longer available as a forage species. In infected areas, redbay trees that are alive are smaller and may not be able to reach maturation (Spiegel 2010) potentially reducing fruit production (Lovett et al. 2006). Redbay was one of the first species fed on when lemurs were initially released on the island; its leaves were fed on for 37% of natural feeding time during the first six weeks of release (Keith-Lucas et al. 1999). Savage (2005) found that redbay leaves, buds, and berries comprised as much as 10% of ring-tailed lemur diets and described it as an "important species." In Coleman's study (2007), lemurs spent 5%, 60%, and 5% of their time foraging on redbay leaves, bark, and stems, respectively. Its loss may cause an increase in the importance of other forage species for fruits, leaves, bark, or stems, necessitating an updated list of forage species.

Foraging by ring-tailed lemurs differs by season in Madagascar (Sauther 1993) and on SCI (Dierenfeld and McCann 1999). In Madagascar, their environment is one that has seasonal characteristics and variability leading to a change in plant species consumed (Coleman 2007; Simmen et al. 2006). Its seasons consist of rainy wet seasons followed by a dry season (Richard and Dewar 1991). In the dry season, forage consists mostly of unripe fruit, mature leaves, and young leaves, while the primary forage in the wet season is ripe fruit (Simmen et al. 2003). Seasonality on SCI is a result of temperature changes as opposed to differences in amount of precipitation. Dierenfeld and McCann (1999) found that ring-tailed lemurs on SCI consumed more seeds in the winter period yet did not change the species on which they foraged. They also found an increase in time spent foraging in winter. Savage (2005), however, found that season did not affect time spent foraging or consuming provisions. But, Savage (2005) found that season did affect the amount of provisions that were consumed by the ring-tailed lemurs, and that the choice of plant species on which to forage varied with season. The differences in the results of these two studies highlight the need to continue studying the effect of season on ring-tailed lemur foraging on SCI.

On SCI, the ring-tailed lemur population provides an opportunity to examine the relationship between introductions and female dominance. My research specifically addressed the following two questions. 1) How does female dominance influence the use of provisions by all members of ring-tailed lemur troops? 2) How does female dominance influence the use of natural resources by all members of the troop? Will female dominance behavior affect who is able to consume provisions and cause other effects on natural foraging behavior or activity budgets? Based on the studies by Savage (2005) and Coleman (2007) as well as results from Keith-Lucas et al.'s (1999) and White et al.'s (2007) experiments, I hypothesized that dominance

behavior of females is affecting lemur provision use and foraging behavior. I predicted that (1) females feed longer at feeding stations thus consuming more provisions, (2) females forage less on natural items than males, and (3) females choose different parts or species of plants on which to forage than males. I also predicted that (4) increasing amount of provisions should increase the time spent consuming provisions and affect activity patterns and natural diet. This experiment consisted of three phases: pre-treatment, treatment, and post-treatment, so effects of doubled provisions on lemur behavior could be determined. The goal was to determine if different amounts of provisions can produce obvious behavioral differences in a population. The purpose of post-treatment was to see if lemur behavior would immediately return to the pre-treatment state following reduction of provisions from doubled to normal amounts.

Another purpose of my study was to identify any combined effects of season and female dominance on lemur behavior. Will a change in seasonal patterns affect the species and maybe require long-term provisioning? My second hypothesis was that season and dominance behavior will interact and have an effect on foraging behavior (food type and species), provision use and activity budget of males and females. I predicted that: (1) females will feed more on provisions, maintaining their dominance over males across seasons, but that both genders will feed on provisions more in winter, (2) time spent in activity types including time spent foraging will differ across season and gender, and (3) percent of time spent feeding on food types and on specific plant species will differ across seasons. Additionally, a secondary objective of my study was to determine if redbay is still consumed and if not, to determine if an alternative natural forage species has replaced it.

CHAPTER 2

METHODS

Ring-tailed Lemur Basic Biology

Ring-tailed lemurs, *Lemur catta*, are found on the south and southwest side of Madagascar historically (Coleman 2007). Today, they are most often found in reserves, especially Beza Mahafaly and Berenty (Cawthon 2005). They live in social groups, are diurnal and occupy a variety of habitats, from closed to open forests and dry to wet areas (Simmen et al. 2006; Wilson and Hanlon 2010). They have a distinctive black-and-white ringed tail that makes them easy to identify (Jolly 1966). No sexual dimorphism exists with size as both genders have an average weight in the wild of 2.2 kg (both males and females), and 2.7 kg in captivity (Cawthon 2005). For females, lifespan is around 18 to 20 years in the wild and in captivity up to 27 years (Gould et al. 2003; Wilson and Hanlon 2010). Male lifespan in the wild is uncertain since they routinely disperse and change groups (Gould et al. 2003). Female *L. catta* breed seasonally and typically only have one offspring at a time, but birth of twins can occur (Jolly 1966; Wilson and Hanlon 2010). Both sexes become reproductively active around 2.5 to 4 years of age (Cawthon 2005).

Ring-tailed lemurs are omnivorous and have been observed foraging on a variety of food items, including various plant non-fruit parts, fruits, insects and sometimes vertebrates (Jolly 1966; Sauther et al. 1999). Plant parts include flowers, stems, bark, leaves, and fruits, while arthropods and vertebrates include grasshoppers, spiders, cicadas, caterpillars, birds, and chameleons (Cawthon 2005). However, plants make up the largest part of their diet. Up to 31%

of ring-tailed lemur diet is fruit according to Yamashita (2008), suggesting that fruit is an important part of ring-tailed lemur diets as an energy source. In Madagascar, the tamarind tree, *Tamarindus indica*, is an important species for ring-tailed lemurs. Its fruits and leaves are consumed all year (Cawthon 2005).

Dispersal patterns differ between male and female ring-tailed lemurs. Male dispersal first occurs when they are between the ages of three and five, and their rates of dispersal (years between moving to new troops) slow as they age. When males first disperse, they may leave on their own or as a member of a group of up to two other males (Sussman 1992). Females remain with their natal group (Cawthon 2005). Troop size varies from as low as three individuals to as high as 27 individuals in areas of intact habitat (Sussman 1977; Gould et al. 2003). In Gould et al.'s study (2003) in Beza Mahafaly, group size averaged 11.5 individuals. Group size increases in areas with supplemented food (Jolly et al. 2002), suggesting that it may be limited due to resource availability. In scrub forest areas of Berenty reserve, average group size is 9.2 individuals (Koyoma et al. 2002), while in tourist areas of Berenty reserve average group size ranges from 12.4 to 16 individuals per group (Jolly et al. 2002; Koyoma et al. 2002). In these tourist areas, the presence of introduced trees, provisions, and a constant supply of water (Jolly et al. 2002) apparently has allowed for an increase in average group size. In 1996, the practice of allowing tourists to feed the lemurs was halted (Jolly et al. 2002). However, they still have access to trash, which accounts for less than 5% of their foraging time (Jolly et al. 2002).

St. Catherine's Island Population

The ring-tailed lemur population on SCI is descended from the six ring-tailed lemurs that were initially placed on the island in 1985 (two males and four females). The next year, six more lemurs were released (5 males and 1 female) (Keith-Lucas et al. 1999). Since then, the

population has increased to approximately 90 individuals in six troops with troop sizes ranging from approximately five to 22 individuals. Adults are equipped with radio-collars that are put on lemurs once they reach adult size (Terry Norton, pers. comm.). Because of differences in climate (and therefore vegetation) between Madagascar and SCI, the lemurs on St. Catherine's are provided provisions daily. Holding pens are located in each troop's home range. Lemurs can freely move into and out of the holding pens except during times of severe cold (Terry Norton, pers. comm.). Daily provisions are provided in food bowls on 2 m tall platforms near and inside their holding pens (Savage 2005). Provisions consist of 30 grams (g) of primate biscuit (Mazuri primate biscuit) for protein, fiber, minerals and vitamins and 30 g of vegetables and fruits, respectively, per animal (<http://www.mazuri.com/mazuriprimatebrowsebiscuit.aspx>). Lemurs are provided one of four different types of fruits (grapes, cantaloupe, apples, and blueberries) and vegetables (sweet potatoes, carrots, yams, and beans) (Royce Hayes, pers. comm.). Since the lemurs were first introduced to the island, the amount of provisions provided has been reduced from 100 g each of fruits and vegetables in 2003 (Savage 2005) to present day amounts.

St. Catherine's Island

St. Catherine's Island is a 5924-ha barrier island located off the coast of Georgia (31°37'50"N 81°9'36.5"W). A forest of mostly oaks, pines and palmetto covers half the island; the remaining habitats include salt marshes and beaches (Keith-Lucas et al. 1999). Average annual temperature on the island is 19.1°C (9.4°C Jan - 27.7°C July), average maximum temperature is 24.7°C (15.4°C Jan - 32.8°C July), and average minimum temperature is 13.3°C (3.4°C Jan - 22.4°C July; Climate Zone 2009). Annual precipitation is 125 cm and average relative humidity is 70.5% (Climate Zone 2009).

Observations

Data sampling occurred in the summer from July 19th 2011 to August 21th 2011. Winter sampling lasted for 10 days, from January 7th to January 16th 2012. The length of both sampling periods was determined based on accessibility to St. Catherine's.

Before data sampling began, I observed the animals and became familiar with established dominance hierarchies by looking for behaviors associated with submission and aggression, feeding priority, and sleeping configuration using an ethogram developed by Tim Keith-Lucas, the primatologist who studied the SCI lemurs for the previous 15 years. I observed lemurs during normal activities beginning at approximately 8 am and ending when they provisioned by staff. The length of the morning observation period was dependent on how long it took to find the troop and when staff gave lemurs provisions (usually between 10am-12pm). I also recorded behaviors during the provisioned feeding period. In the afternoon, I observed lemurs beginning at 3-5pm until they retreated to their sleep site or it became too dark for observations. To find the troops for observation, I used a radio tracker and prior knowledge of troop behavior, and when found, I used binoculars to observe them in trees. I was able to recognize individuals due to their color-coded radio-collars; subadults without radio-collars had parts of their tail shaved in a unique pattern for identification.

Four troops were observed in summer (Table 1). Three groups were observed in winter (n=13) (Table 2); one troop from summer was excluded due to their quarantined status. Two other troops (Yankee Bridge and Windmill) were not observed in either season due to their large size and difficulties in accurately observing their behaviors. I did not record data for infants or for behavior during rain because lemurs were inactive.

I used focal and instantaneous scan sampling methods to observe lemur foraging behavior when provisions were not present (Altmann 1974) in both summer and winter. Focal samples were conducted haphazardly on individuals (subadult or adult only, no infants) for 5 min. Aside from a few rare occurrences, focal scans were conducted on all individuals of a group each time the group was observed. I recorded behaviors and classified them as active (without foraging), inactive, and foraging. I considered walking, climbing, self-grooming, grooming, play, and drinking to be active behaviors while inactive behaviors consisted of sitting and sleeping. Foraging included anything involving consumption of food. When recording foraging, I recorded plant species and food type (fruit, leaves, stems, bark, etc). If an unknown species was eaten, a sample of that species was collected for later identification. The following items were recorded as miscellaneous: pine cones, pollen parts, unknown, stems, bark, and flowers. After a cycle of three focal observations, I conducted an instantaneous scan on all individuals and behaviors of each individual were recorded, using the same categories as focal scans. If a specific individual could not be identified or spotted, their behavior was not recorded during instantaneous scans. I calculated percent of time spent foraging, active, and inactive for each individual, as well as percent of time spent on specific species and plant parts.

Each day when provisions were provided between 10 to 12 a.m., I used scan sampling to record which lemur(s) was present at that food bowl (termed provision site) every 15 seconds (Altmann 1974). Individuals who were recorded at food bowls were eating provisions. Feeding posts are found at various locations near the troop's home site, but the number of feeding posts at each troop's location is not proportional to troop size. However, the number of food bowls and total amount of food distributed is proportional to troop size (Terry Norton, pers. comm.). Food bowls were placed on the ground or inside holding pens for consumption when there were too

few feeding posts. Scans at provisioned feeding sessions lasted until lemurs finished eating, usually around 12 to 1 p.m. Percent of time spent feeding on provisions was calculated for each individual out of the total time food was present.

I collected data in three phases in summer. The pre-treatment phase, which consisted of lemurs receiving their normal provisions, continued for 14 days from July 19 - August 3, 2011. The following week, termed the treatment phase, provision amounts were doubled to 60 g each of primate biscuit, fruits, and vegetables. This phase lasted for eight days from August 3 to morning of August 10, 2011. At the conclusion of this phase, amount of provisions was returned to normal. This final phase, termed post-treatment, lasted for twelve days from the afternoon of August 10 to August 21, 2011. In the winter, amount of provisions was not doubled. Therefore, I collected data in one phase during the winter, from January 7th to January 16th 2012.

Data Analysis

To test my first hypothesis, data were collected during three phases in summer 2011. To test my first prediction that provision use will differ across gender, I collected provision data across all three phases and compared within phases to look for gender differences. Each individual provisioning session was also divided in half during analysis in order to determine whether or not females consumed more provisions initially but not towards the end of the feeding period. For my second prediction that females would forage less on natural forage than males, data were collected for activity type in all three phases and compared within phases to assess gender differences. For my third prediction that females choose different parts or species of plants on which to forage than males, food type and plant species data were collected during foraging sessions in all three phases and analyzed within phases to look for gender differences. For my fourth prediction that increased amount of provisions would affect behavior, across phase

analyses were conducted for provision use, activity budget, food type and plant species to assess gender differences.

To test second hypothesis (differences in behavior between seasons), I collected data during the winter and compared the data to the pre-manipulation summer period. Only the groups and individuals found in winter were used in comparisons with summer data. In tests of summer only, all four troops were used. In comparisons with winter, the data from the East Road troop were excluded since there was no winter counterpart. To test my first prediction concerning differences in provisioning across season and gender, I collected provision data in both seasons and compared within each season to identify dominance and across season to assess change in percent of time at provisions. For my second prediction that activity type patterns will differ across season and gender, I collected data regarding activity types in both seasons and analyzed within and across seasons to identify any differences. To test my third prediction that food types will differ across season, I collected food type data during foraging sessions and analyzed within and across seasons to identify any differences. For my fourth prediction that plant species consumed differs across season, I collected plant species data and recorded which plant species were consumed and analyzed within season to compare and identify any differences.

Data analysis consisted of one-way, two-way, and repeated measures ANOVAs, calculated using JMP®Pro 9.0.0 (2010). Sessions of provisioning were analyzed overall and then divided in half to analyze differences between halves. Data were sorted into first and second halves, and a percent of time spent consuming provisions in each half was calculated for both genders. For plant analysis, some species were excluded due to low percentage of forage time (<5%) while others were excluded due to statistical test complications. For plant species,

“unidentifiable” represents a group of multiple species unable to be recognized. Data for time spent in behaviors and provision scans were analyzed as percents and arcsin transformed in order to meet parametric test assumptions. Other transformations such as $\cos(10 + \text{percent of time})$ were used when arcsin was unsuccessful. Repeated measures ANOVAs were used to analyze time of day, phase and seasonal differences. Two- and one- way ANOVAs were used to analyze differences within gender, phase, and season. If results were significant, Tukey HSD tests were done to determine further differences.

CHAPTER 3

Results

In the summer, I observed the behavior of 21 lemurs in four troops. For provisioning in the pre-treatment phase, the four troops were sampled approximately 6 hours and had an average provisioning session of 25.5 minutes. In the treatment and post-treatment phases, I sampled the troops for approximately 3.5 and 3.7 hours with an average provisioning of 30 and 24.5 minutes, respectively. For focal scans in the pre-treatment phase, I sampled the four troops, including adults and subadults, approximately 32.3 hours (Females: 19.8h; Males: 12.5h). I observed Picnic Bluff for two mornings and three afternoons (Total: 6.2h; F: 3.3h; M: 2.9h), Terry Lynn for three mornings and afternoons (T: 8.3h; F: 5.2; M: 3.1), and Engineer and East road for four mornings and three afternoons each (Engineer – T: 7.4h, F: 4.8h, M: 2.6h; East Road – T: 10.4h, F: 6.5h, M: 3.9h). In the treatment and post-treatment phases, I sampled the four troops, including adults and subadults, for approximately 24.2 (F: 13.8h; M: 10.4h) and 24.7 (F: 15.5h; M: 9.2h) hours, respectively. In the treatment phase, I observed Picnic Bluff, Engineer, and East road for two mornings and afternoons each (Picnic Bluff – T: 8.5h, F: 4.2h, M: 4.3h; Engineer – T: 7.2h, F: 4.4h, M: 2.8h; East Road – T: 5.3h, F: 3.2h, M: 2.1h) while Terry Lynn was observed one morning and afternoon (T: 3.2h; F: 2h; M: 1.2h). In post-treatment phase, I observed Picnic Bluff and East road for two mornings and one afternoon each (Picnic Bluff – T: 4.8h, F: 2.5h, M: 2.3h; East Road – T: 5.5h, F: 3.6h, M: 1.9h) and Terry Lynn and Engineer for two mornings and afternoons each (Terry Lynn – T: 7.3h, F: 4.8h, M: 2.5h; Engineer – T: 7h; F: 4.6h, M: 2.4h).

In winter, three troops and a total of 13 individuals were sampled. For provisions, only two troops were sampled (Engineer and Picnic Bluff) since Terry Lynn troop did not feed on

provisions. Due to a shorter study period, less time was spent observing individuals in winter than summer. These troops were sampled for approximately 1.5 hours combined with an average provisioning session of 18.2 minutes. For focal scans, the three troops were observed a combined approximate total of 19.5 hours (Females: 12.2h; Males: 7.3h). The three troops were sampled the following number of times: Terry Lynn, two mornings and three afternoons (T: 5h, F: 3.1h, M: 1.9h); Engineer, three mornings and afternoons (T: 5.4h, F: 3.8h, M: 1.6h); and Picnic Bluff, three mornings and afternoons (T: 9h, F: 5.2h, M: 3.8h).

To maintain consistency, the same three troops used in winter (Engineer, Picnic Bluff, and Terry Lynn) were used from summer for seasonal comparisons. The three groups in summer consisted of an approximate total of 4.2 hours of provision samples (average provision session = 26.7 minutes) and 21.9 hours for focal scans (Females: 13.3h; Males: 8.6h).

Summer and Amount of Provisions

Provision Use

My first prediction was that dominant females would spend more time at provision sites than males. For provision use in the pre-treatment phase, females spent a significantly higher percent of time at provision sites than males (Figure 1; Table 3). This was because they spent significantly more time at the feeding bowls in the first half of feeding sessions than males did (Table 3). Females arrived at provision sites first the majority of the time, and if a male was there first, then a female displaced him quickly. Aggressive encounters between males and females during provisioning sessions occasionally occurred. In the second half of provisioning periods, males and females spent approximately the same percent of time at provision sites (Table 3). Overall, a higher percent of time was spent at provision sites in the first half than the second half (Table 3).

Activity Budgets

My second prediction that activity patterns would differ between genders due to provisioning differences was not met. For activity type in pre-treatment phase, all three activity types were significantly different from each other with the highest percent of time spent inactive and lowest time spent foraging (Table 5). The interaction between individual (categorized as female or male) and percent of time spent in each activity had a significant effect on percent of time spent in each activity but a Tukey HSD test did not show a difference in the means (Figure 2; Table 5). Therefore, gender did not affect percent of time spent in activity types.

Diet

Since females spent more time at provisions sites, I predicted males would feed on different food items and plant species than females when foraging naturally. For food type versus gender, food types were classified as acorns, soil, ET (leftover provisions), fruit, leaf, and miscellaneous (pine cone, unknown, stem, bark, and flower). In pre-treatment phase, there was no difference in percent of time spent consuming food types (Table 5) or between genders consuming each food type (Table 5). In the pre-treatment phase, only two species were analyzed (*Quercus* and *Vitis*). *Quercus* food items (specifically acorns) were fed on a significantly higher percent of time than *Vitis* (Table 6). No difference was found for the interaction between species and gender (Table 6). Males and females spent the same percent of time foraging on plant species.

Effects of Doubled Provisions

My fourth prediction was that increasing amount of provisions would affect lemur behavior. I predicted that doubling provisions would affect time spent at provision sites, activity patterns, and foraging behavior, which was partially met. In the treatment phase, males and

females spent approximately the same percent of time at provision sites (Table 3). During the treatment phase, a significantly higher percent of time was spent at provision sites by females in the first half (Table 3). In the second half, females and males spent the same percent of time at provision sites (Table 3). A higher percent of time was spent feeding in the first half than the second half for both genders (Table 3).

In the post-treatment phase, I predicted that behaviors should return to the pre-treatment averages. In the post-treatment phase, I observed the same pattern in feeding on provisions that I had observed in previous phases. Females spent more time at provision sites overall, more time at provision sites in the first half of a provisioning period, but the same amount of time as males during the second half of the provisioning period (Figure 1; Table 3).

Phase (pre-treatment, treatment, and post-treatment) did not significantly affect percent of time spent in each activity type. For females, there was no change in the percent of time spent active, foraging, and inactive. Males exhibited the same pattern (Table 4).

In the treatment phase, there was a significant effect on time spent consuming food types, but the Tukey HSD test showed no difference among individual food types (Table 5). Males and females ate the same types of food (Table 5). For the post-treatment phase, no difference was found in percent of time spent consuming food types or between genders consuming each food type (Table 5). The following plant species were observed to be eaten by lemurs: *Arundinaria*, *Liquidambar*, *Morella*, *Pinus*, *Pterocaulon*, *Quercus*, *Sabal*, *Tillandsia*, *Vaccinium*, *Vitis*, and unidentified. In the treatment phase, three species (*Vitis*, *Morella* and *Quercus*) were analyzed. *Quercus* was eaten a significantly higher percent of time than *Vitis* and *Morella* (Table 6). The interaction between species and gender was not significant (Table 6). Males and females spent the same percent of time foraging on plant species. In the post-treatment phase, three species

(*Quercus*, *Vitis*, and *Vaccinium*) and unidentified were analyzed. *Quercus* and *Vitis* were eaten a significantly higher amount of time than unidentified and *Vaccinium* (Table 6). The interaction between gender and species was not significant (Table 6). Males and females spent the same percent of time foraging on plant species.

Seasonal Effects

Provision Use

I predicted that provisioning use would differ in summer and winter. In winter males and females spent the same percent of time at provision sites. Season did not affect percent of time males or females spent at provision sites (Table 7). But, of the four total provision feeding sessions, males and females were first at provision sites the same amount of time, in contrast to summer.

Activity Budgets

Following my first prediction, I predicted that activity patterns and foraging time would differ in winter. With all troops combined in winter, a significantly higher percent of time was spent inactive and less time was spent foraging. No difference was found between the interaction of gender and activity type (Table 8). Gender did not affect percent of time spent in activity types.

For Terry Lynn troop in summer, a significantly higher percent of time was spent foraging and less time was spent inactive. In winter, all activity types had about equal time spent (Figure 3; Table 8).

For Picnic Bluff troop in summer only, a significantly higher percent of time was spent inactive and less time spent foraging. In winter only, percent of time spent foraging was significantly less than inactivity and activity (Figure 3; Table 8).

For Engineer troop in summer, all three activity types were significantly different from each other with most time spent inactive and less time spent foraging. The same pattern was seen in winter (Figure 3; Table 8).

Comparing across seasons, a significantly higher percent of time was spent active in the summer for all individuals, and overall males were more active than females. A significantly higher percent of time was spent foraging in summer with no difference between males and females. Percent of time spent inactive was significantly higher in winter with no difference between males and females (Figure 4; Table 8).

Female percent of time spent active was significantly higher in summer than winter. Percent of time spent active in males did not differ by season. Females spent a significantly higher percent of time feeding in summer while males had no difference for season. Females had a significantly higher percent of time spent inactive in winter while males showed no significance for season (Table 8).

Diet

In winter, acorns were fed on a significantly higher percent of time than miscellaneous and leftover provisions (Table 9). The interaction between food type and gender was not significant (Table 9). Males and females spent the same proportion of time eating different food types. For females only, a higher percent of soil was consumed in summer (Table 10). No food type was consumed more across season for males (Table 11). In the winter, three plant species were analyzed (*Quercus*, *Morella*, and *Sabal*) (Table 12). *Quercus* was eaten a significantly higher percent of time than *Morella* and *Sabal*. *Morella* and *Sabal* were fed on the same amount of time. Interaction between species and gender was not significant. Males and females spent the same percent of time consuming different plant species.

CHAPTER 4

Discussion

Summer and Provisioning Use

The clearest effect of gender was found in consumption of provisions in the pre-treatment phase. Females spent more time at provision bowls throughout the feeding period supporting my first prediction that dominance behavior would influence amount of time spent at provision sites. Males near stations of provisions were routinely displaced by females and often waited until females had finished before beginning to feed, confirming a dominant status for females. Towards the middle of feeding sessions, females became satiated but still spent a significantly higher percent of time at provision sites than males. Instances where males and females shared a bowl of provisions were rare. These results are the first documentation of a difference between genders in time spent feeding on provisions on St. Catherine's Island since Coleman did not find a difference (2007). I observed that males sometimes rushed the bowls of provisions once they were distributed to grab food and were met with aggression or chased away by females. Some males also ran off from a bowl of provisions when a female approached thus avoiding any confrontation. In a study on patch size, females fed more than males in small patches, but as patch size increased, males and females spent the same amount of time feeding (White et al 2007). The alpha males did not attempt to feed in the two smallest patches. Adult males in my study seemed to avoid feeding during the early stages of provisioning sessions unless there was an open bowl available. Males in Coleman's (2007) study also were noted to wait for females to finish before feeding on provisions. The benefit to having this priority access to provisioning for females is reduced competition from males. If natural foraging was limited or non-existent on

the island, it appears that females, at least with the amount of provisions currently provided by zoo staff, would be able to consume what they desired while males could not. Natural forage, in this case, could be critical to the health of males and other subordinate individuals.

Because females spent more time at provisions than males, I predicted that males would need to spend more time consuming natural forage. However, this was not the case, nor did they feed on different food types or different plant species. The lack of difference between genders suggests that females are not dominating males during natural foraging activities, possibly due to patch sizes. In large patches, females are known to exert less control (White et al. 2007). If an introduction site had small patches and lacked provisions, males could be impacted. In such a case, females could consume the high quality food sources leaving males with limited resource access, poorer quality resources, or lack of certain resources entirely. Male health could then be compromised, which would pose problems for the long-term sustainability of the group.

It is interesting to note that despite spending more time at provisions, no difference was found in time spent foraging on natural foods between genders during the summer. Males are not making up for the deficit in provisioned food by spending a higher percent of time foraging. This could be due to increased resource need by the females as during this time they were still carrying their infants and lactating (Sauther 1998, Savage 2005). Lactation is energetically expensive (Tilden and Oftedal 1997), and carrying infants is energetically expensive. Males do not help with infant care and thus may have lower energy needs than females during this time.

My third prediction that food type use and plant species eaten would vary with gender was not met. With the difference in time spent feeding on provisions, it was expected females would consume more provisioned fruits, leaving less for the males that would result in males spending more time feeding on natural fruit. No differences in food type were found between

genders in the pre-treatment phase. With plant species, lemurs in pre-treatment phase (both genders) preferred *Quercus* over *Vitis*. Acorns were a popular food item explaining the high percentage of *Quercus* fed on in this study and all previous studies (Coleman 2007; Savage 2005). *Vitis* was eaten for grapes constituting a part of their fruit diet. Percent of time spent consuming *Vitis* in my study is roughly consistent with Savage's (2005). Acorns have a high fat content and fruits have high carbohydrate content (Dierenfeld and McCann 1999). Since late summer is in between the costly birthing/lactating and late-lactating/weaning time (Sauther 1998; Savage 2005; Tilden and Oftedal 1997), it may explain the importance of *Quercus* and *Vitis* in lemur diet. My study is the first to quantify soil in ring-tailed lemur diet on SCI. This behavior has been reported in the wild (Sauther et al. 1999). Coleman (2007) found *Quercus* and *Sabal* as the dominant species eaten between August and December. *Sabal* and *Vitis* are both fed on mostly for fruits, so the difference between our studies may be a result of seasonal abundance. While a significant difference for food type was not found in my study, there is enough uncertainty due to low samples and high standard error to warrant further studies and for this to be a consideration when searching for suitable locations for future translocations.

Doubling provisions partly met my fourth prediction that time spent at feeding bowls would increase. It allowed males to spend the same percent of time at provision bowls as females. As in the patch size study (White et al. 2007), when amount of food increases, males and females spend the same amount of time foraging. Females did maintain their dominance and priority of access by feeding significantly more than males in the first half of a provisioning session. In the post-treatment phase, when provisioning returned to the normal amounts, the overall difference between males and females returned. But, the pattern observed during the treatment phase that males and females foraged equally in the second half of the feeding bout

remained. It seems that males increased in percent of time spent at provision sites beginning in the treatment phase which carried over into the post-treatment phase. Apparently amount of provisions can influence amount of time males will spend at food bowls but does not eliminate female dominance behavior. Even if managers know females dominate provisions, it is important they also understand that adding more provisioned food will not guarantee its equal distribution among genders.

Doubling provisions did not result in a change in the pattern of percentages of time spent active, inactive, and foraging overall in either gender. Thus my fourth prediction, that doubled provisions would affect activity patterns, was not supported. I predicted that doubled amounts of provisions would lead to increased inactivity and decreased activity, but this was not the case. This suggests that amount of provisions does not change natural foraging behavior or activity levels. The lack of a difference could be due to the short duration of treatment or post-treatment phase.

In the treatment phase, no difference was found among time spent consuming food types, and doubled provisions did not significantly affect percent of time spent feeding on plant species. However there were some non-significant changes in percent of time spent on food types and plant species from pre-treatment phase which could indicate effect of provision amount. Females spent a lower percent of time consuming acorns and fruit and an increase in percent of time spent feeding on leftover provisions. Males also had a reduced percentage of time spent feeding on fruits and slightly more time on leftover provisions. This is consistent with the apparent drop in consumption of *Vitis* and continued dominance of *Quercus*. Reduction in time spent feeding on *Vitis* was associated with the increased amount of fruit provisions as *Vitis* was consumed mostly for its fruit. Lemurs were seemingly able to meet all of their fruit needs via

provisions and fed more on leftover provisioned food overall rather than foraging naturally to meet their food needs thus partially meeting my fourth prediction that doubled provisions will affect foraging behavior. In future translocations, if too much provisioned food is given, my results indicate the possibility fewer natural items will be eaten. Since lemurs need to test species when first released, excess provisioning could hinder the development of their natural diet.

In the post-treatment phase only, *Quercus* and *Vitis* were fed on the same amount of time and no difference was found between genders. Compared with food type, fruits and acorns are fed on roughly the same amount of time explaining the equivalence of *Vitis* and *Quercus*. These two species dominated the lemur diet, accounting for over 80% of total food species consumed. The change in relationship between *Quercus* and *Vitis* is surprising and could be a delayed result of the doubled provisioning or a result of ripened *Vitis* fruits. However, since both species produce fruits and acorns that are used as energy sources (Dierenfeld and McCann 1999), it does not necessarily represent a significant shift in diet.

Because only a slight change in behavior resulted from a doubling of provisions, and because my results were similar to Savage's (2005) findings when provision amounts were 100g for fruits and vegetables per individual, it seems provision amount does not change plant species consumed but does affect time spent consuming natural fruits. In Savage's (2005) study, natural fruit was still eaten which was not the case in my study. I did not observe lemurs eating any natural fruit during the treatment phase of my study. One possible explanation for this difference is that the lemurs in Savage's study were accustomed to higher amount of provisions and were eating more than needed. When provision amount was doubled in this experiment, individuals were not used to the increased food and were more satiated, requiring less natural items. One

way to test this in the future would be to carry out the treatment phase for a longer period of time to see if lemurs eventually develop more of an appetite and consume more natural forage along with the provisions.

Seasonal Effects

Consumption of provisions differed in the winter although in an unexpected manner. While percent of time spent feeding did not differ for either gender across season, males and females were found to feed a similar amount of time in winter, a change from the female-dominated summer. According to my first prediction, females were expected to feed more on provisions and maintain their dominance over males across seasons when consuming provisions and both genders were expected to feed more on provisions in winter. My results do not meet these predictions since there was (1) no difference in percent of time spent consuming provisions between males and females, suggesting that females are not exerting their dominance in the winter and (2) no change in percent of time at provision sites for either males or females. Lack of difference across season is consistent with results from Savage's study even though the amount of provisions was higher per animal in her study (2005). Observations of the troops' behavior suggest provisioning is overall less important in the winter season. Individuals at Picnic Bluff and Engineer did not rush for the provisions as they did in the summer and instead seemed uninterested by remaining inactive or engaging in other behaviors such as grooming. In contrast, in the summer they rushed the bowls when they were distributed to begin eating. Terry Lynn troop was not observed in the vicinity of their provision station for the duration of the winter session, providing further evidence that lemurs are less interested in provisions.

A biological cause could be due to the lack of dependent offspring in winter versus the summer. Savage found that provisions were depended on most in April through July during the

period of birth and lactation (2005), so the apparent lack of interest in winter provisions is consistent with her findings. Fruits are abundant in the wild during the birth and lactation time (Sauther 1998) and thus foraged on by females during this time. An increased need for fruits by females on St. Catherine's Island would prompt increased interest and desire for provisions in summer because it is during the birthing and lactating period. Therefore in winter, without this pressure, it seems dietary needs can be met with less reliance on provisioning. Future translocation efforts need to take into consideration possible seasonal changes in resource requirements for females by ensuring proper availability of forage or extra provisions during lactation.

My second prediction that time spent in activity types, including time spent foraging, will differ seasonally by gender was partially met. Summer and winter activity patterns were similar overall but with some differences. Overall, lemurs were more active, foraged more, and were less inactive in summer than winter. These results are similar to those of Savage's (2005) on SCI and Rasamimanana et al.'s (2010) from Berenty Reserve. Compared to Coleman's results (2007), lemurs in my study foraged more overall as she found an 11.1% overall feeding time including natural forage and provisions. My results for summer foraging rates were similar to those of Dierenfeld and McCann (1999) who found a feeding rate of 19.7% for natural items, but my winter foraging rate was less than their winter foraging rates. From this, my results seem to suggest possible yearly variation in time spent foraging.

Rasamimanana et al. (2010) found low energy expenditure (measured by distance traversed by the troop) in the gestation period. On SCI, gestation occurs during the winter (Keith-Lucas et al. 1999), and females in my study were less active in winter. Females exhibited this change in percent of time spent active across seasons while males did not. This could be

explained by the amount of self-grooming (an active behavior) which they performed in the summer. This behavior is used as a cooling mechanism and since females were still carrying around their infants, they are warmer in summer (Terry Norton pers. comm.). In the winter, staying cool was no longer an issue. In fact, they huddle together in trees to stay warm. These results suggest males are not as affected by the change in season as females in regards to activity type highlighting a difference between the genders which is consistent with Rasamimanana et al.'s (2010) findings where female activity patterns changed with reproductive periods.

Activity levels differed in the different troops. Both Picnic Bluff and Terry Lynn had different activity patterns compared to the combined data. Picnic Bluff troop spent the lowest time foraging and the same percent of time spent inactive and active. Compared to their summer results, this was a change. Terry Lynn troop had the most drastic change from the normal pattern where they spent roughly the same amount of time inactive, active, and foraging, most likely a direct result of the absence of provisioned feeding. This troop was not found in its home site at all for the duration of the winter session, was not observed feeding on provisioned food and apparently did not engage in feeding on given provisions. Instead they foraged naturally, accounting for some if not all of the increase for foraging and their increase in activity. For Picnic Bluff, even though they ate provisions, they still may have needed to spend more time searching for food. Most flowers bloom in summer and spring (Coleman 2007) so the idea of scattered forage species and increased search time is plausible. Also, habitat may differ between the troops and explain why certain troops need to spend more time searching for food while others do not.

My third prediction that percent of time feeding on food types and plant species will differ across seasons were partially met. Within winter, acorns were eaten more than

miscellaneous items (pine cones, pollen parts, unidentified, stems, bark, and flowers) and leftover provisions but not significantly more than leaves and fruit. This is in contrast to the lack of a difference found in percent of time food types consumed in summer. Based solely on observations, acorns were the favorite food for lemurs during winter. In winter, it has been found that choice of which plant item to feed on is based more on availability (Ganzhorn 1986). This could explain the shift to *Morella* and *Sabal* in winter from *Vitis*. Availability could also explain the preference for acorns which may simply be a result of its abundance since other fruits and flowers are more abundant in spring and summer (Coleman 2007), acorns are produced this time of year (Coleman 2007), and overall *Quercus* species are widespread across the landscape. However, acorns do have a high fat and protein content which is beneficial as a calorie and energy source (Savage 2005; Dierenfeld and McCann 1999) so it is a quality resource. My results differed from Savage's (2005) study where only one troop seemed to feed a large amount of time on acorns (average= ~30%), another had a smaller amount (average= ~10%), and the third did not feed on them at all. This could be due to dietary preference changes or another unidentified change with the implication that lemur diets may change through time. *Morella* was eaten for its leaves, and its apparent increase is consistent with Savage's study (2005). *Sabal* was eaten for its fruits that serve as another energy source (Dierenfeld and McCann 1999). Compared with Savage's study (2005), *Vitis* was not fed on at all during the January month indicating its availability is limited to non-existent during this time. The fact it was in the current study could be due to yearly changes in climate (i.e. warm winter) or a spread of this species in recent years.

An interesting finding was that females ate soil in the summer but not the winter, and that males did not eat soil in either season. Soil could be eaten as a source for sodium, which has

been found to be low in ring-tailed lemur diets on SCI (Dierenfeld and McCann 1999). This seasonal intake of soil by females could reflect a need for nutrients since they are lactating during the summer (Savage 2005).

Savage (2005) found that as the year progressed, variation in forage items fed on changed. Dierenfeld and McCann (1999) found seeds (acorns) were seasonally consumed which is consistent with my results since my entire study occurred when acorns were abundant while their study took place across an entire year. Coleman (2007) found that most of the spent time feeding on natural items was spent feeding on fruit (58%), a higher amount of time than in my study. Around this time in Savage's study (2005) there was also a spike in percentages of *Sabal* items eaten. The higher percentage in Coleman's study is therefore likely due to her study period which consisted of the late lactating and weaning period of October and November when there is an increase in fruit availability (Savage 2005; Sauther 1998). My results reflect the variability in feeding among ring-tailed lemurs, which is similar to the flexibility in diet in wild, captive and semi-free ranging conditions (Dierenfeld and McCann 1999; Ganzhorn 1986; Sauther 1998). Ganzhorn (1986) has described them as having adaptability to environmental changes as well as being opportunistic when it comes to foraging, and Sauther (1998) found accessibility of forage species to affect patterns of foraging thus supporting the variable results found in this study.

Fewer species were consumed in winter (six) versus the combined phases of summer (ten) and this pattern was also observed by Dierenfeld and McCann (1999) in an earlier study on St. Catherine's Island and in the wild (Sauther 1993). Since more species produce fruits and flowers in the spring and summer on St. Catherine's Island (Coleman 2007) it could explain the change in number of plant species fed on. My results are consistent with Coleman (2007) who

found *Quercus* spp and *Sabal* to be the highest overall species fed on and low percentages for the other species recorded in my study. This is different from Dierenfeld and McCann (1999) who found *Celtis*, *Juniperus*, *Melia*, *Persea*, and *Sabal* to be the most important plant genera. *Quercus* has been found to be a dominant forage species in late summer before (Coleman 2007; Savage 2005), and now it is clear it is an important species in winter too.

Compared with past studies, there were some differences in plant species eaten (Table 13). The most notable change appears to be the low number of observed species consumed in my study. This could be explained by differences in the time of year the studies were conducted. My study was limited to three months while three of these past studies were conducted for at least a year (Dierenfeld and McCann 1999; Keith-Lucas et al. 1999; Savage 2005), and Coleman's (2007) was conducted from August through December. Since I had observations consisting of unidentifiable species, it is likely some of past species were foraged on which I was unable to identify. The results of these studies suggest ring-tailed lemurs on St. Catherine's Island have a flexible diet (about 40 genera) and are able to survive on different species.

Another interesting result is the lack of redbay, *Persea borbonia*, in diet in both seasons. This was expected due to the spread of laurel wilt disease (Koch and Smith 2008), but the absence of redbay from their diet entirely shows the impact it has had. In past studies, redbay was fed on for leaves, bark, buds, and berries (Savage 2005; Coleman 2007). Dierenfeld and McCann (1999) found redbay to be one of the five most important plant species to lemurs. The absence of it near four of the six troop sites should be telling of the drop-off of the species considering its past abundance (Coleman 2007; Dierenfeld and McCann 1999; Savage 2005). In comparisons with past studies, my results show no obvious differences directly as a result of the

loss of redbay. Savage (2005) and Coleman's (2007) studies showed less emphasis of redbay in lemur diet compared with Keith-Lucas et al. (1999) and Dierenfeld and McCann's studies (1999). It seems lemurs have been gradually adjusting diet away from redbay, explaining the lack of clear differences in time fed on forage species in my study.

Season has an effect on plant species consumed by ring-tailed lemurs on SCI although gender does not seem to have a strong influence on plant species consumed. The seasonal changes reflect availability of forage and possible change in dietary needs of lemurs. Lemurs appear able to adjust to seasonal availability of plant species and food types to meet their needs. My results suggest percent of food types consumed for each gender may vary seasonally, and specifically, females may need different food items across the year as they go through pregnancy, birth and lactation. Future translocations need to adjust for these changes and ensure the habitat has species that produce items that will meet the lemurs' needs. Specific species do not appear necessary as they show flexibility in diet and capable of surviving the loss of a forage species.

Conclusions

Any form of translocation is a complicated process and requires as much information as possible. My study provides valuable information that can be used in future ring-tailed lemur translocation projects. Considering Richard Branson has already begun introducing lemurs in the Caribbean (Black 2011), it further shows the importance of understanding ring-tailed lemur translocation biology. My results reveal the link between provision use and female dominance, which must be accounted for in future translocations.

Despite differences in time spent at provision sites, males and females seem to have the same diet regarding natural forage items during their normal conditions on the island. It seems

females need more food during the summer, and due to female dominance, they can control provisioning and consume as much of it as they can over males. My results provide additional support for White et al.'s (2007) findings that females monopolize small food patches. This behavior ensures females will have food even during times of deficiency, a critical advantage over males.

Ranging on SCI was found to be correlated with feeding on new plant species (Keith-Lucas et al. 1999). My results found provisioning was a preferred food so if it is not carefully managed, lemurs can overly rely on provisions and not explore the habitat as much. When this occurs they will test fewer species and not have a diverse natural diet. If a disparity exists between males and females in amount of provisions eaten, then it could result in males foraging naturally and testing species but not females. Coleman (2007) found that introduced males in her study group were able to adjust quickly and find suitable species to eat by following the females. However the reverse may not occur since females are the ones who lead the troop to forage sites (Sauther 1993), and they may not follow the males' lead. Savage found provisioning did not inhibit sensitivity to forage availability (2005) but this was not compared between genders. Provisioning use does differ with gender and could have effects on response to forage availability. When ring-tailed lemurs were initially released on the island, they fed on two species (*Persea borbonia* and *Vitis rotundifolia*). Their diet then increased to four species in the first six weeks and fourteen after that, but they still spent 83% of their time feeding on provisions (Keith-Lucas et al. 1999). Their natural diet has grown through the years to include over 40 species (Coleman 2007; Dierenfeld and McCann 1999; Savage 2005). This shows the importance of providing lemurs provisions initially and in equal amounts for all individuals but not a high enough amount to prevent natural foraging.

If provisioning were removed on SCI, females would seemingly need to adjust to this and forage more on natural items. The exact effect of removing provisions cannot be known until it is absent and studies are conducted. In Savage's study (2005) a roughly 50-50 split was found between time spent consuming provisions and natural forage items. In Coleman's (2007) study, she found a 58-42 split but with consideration to disturbances during observations, she said it would be closer to Savage's results. While amount of provisions given has changed in the time since Savage's study, this still suggests removal of provisions will result in a maximum of doubled feeding rate on natural items. Given the importance of provisioning in introductions (Fischer and Lindenmayer 2000; Konstant and Mittermeier 1982; Tear and Ables 1999), it is vital to understand how it relates to natural forage and behaviors of animals involved. These results add more information about this relationship in a population of individuals that act as a model system for translocation projects. In future management and translocation projects, care should be taken to ensure the appropriate amount of provisions is given to suit the lemurs' needs in that location.

Amount of provisions does seem to affect female dominance behavior providing a direct link between them that should be considered in future translocations. If a small provision amount is given, females could consume all of this resource leaving none for males potentially causing detrimental effects. Carefully increasing amount of provisions can correct for this. By comparing percentages of time spent on food types, it becomes obvious that amount of provisions is playing a role. Natural fruit was not fed on during the week of the treatment phase and females experienced a spike in feeding on leftover provisions compared with pre-treatment phase. In the post-treatment phase, fruit was consumed naturally again and leftover provision time spent returned to levels similar to what was found in pre-treatment phase. This suggests

provisioned food is the favorite food source for at least females and when present they will feed on that more in the afternoon and less on natural items. It then follows that if too much food is given as provisions then individuals may not forage as much on natural items as my results seem to indicate. This could be exclusive to females or found in both genders but requires future study.

Season clearly has an effect on behavior of lemurs in regards to activity type, provisioning, and diet. This is the first study conducted to look for seasonal differences between genders. Males and females spent the same percent of time at provision sites and overall showed a lack of interest, a drastic change from summer. While activity type did not have any obvious relationship to female dominance, females did experience seasonal changes in activity types while males did not. Forage items fed on could vary by seasons and gender thus reflecting the varying needs of males and females throughout the year. *Quercus* was fed on in large quantity in both seasons but there were differences in number of plant species eaten. Also based on observations alone, *Vitis* was eaten less in winter and more of *Morella* and *Sabal* were eaten. This difference is likely due to availability in these seasons (Coleman 2007), but it shows the versatility of lemurs in diet. The lemurs in my study were able to adjust to seasonal availability of forage and plant species, but it is critical to compile a complete seasonal list of available forage in order to ensure lemurs have enough food throughout the year.

Lemur behavior is changed by season and these effects are important to keep in mind in future translocation and management decisions. Some plant species that are not winter deciduous are needed to ensure they have enough food to forage on naturally. These plants should produce an item that is high in fat or carbohydrates since they have most time consumed and are important for energy sources (Coleman 2007; Dierenfeld and McCann 1999). Selecting

food based on sugar was not observed to be the case in Mowry and Campbell's study (2001) but this could be due to amount of provisions. This has changed since their study and my earlier results indicate amount of provisions can affect food types consumed so a preference for items with high sugar content (fruits) could now be occurring since fewer provisions are regularly given to ring-tailed lemurs now. If the location is deficient in winter forage, particularly ones high in fat or carbohydrates, simply providing provisions may not be enough to sustain them, and they should be monitored during this time. Factoring in the dominance behavior of females, if provisions do become the main food source in winter then females could consume most of this resource, which could be an issue for males. Activity type changes across seasons should not be much of a management issue since nothing too drastic occurred. Ring-tailed lemurs appear to be excellent candidates for translocations due to their basic biology, so it is essential we continue to study their behavior to better understand it and allow for these projects to be successful. Since many species of lemur have been found to exhibit female dominance or only have a feeding priority, these considerations are relevant to any of their future translocation projects (Pereira et al. 1990; Young et al. 1989).

Future Directions

In future studies, a team should try and record the foraging habits of all of the lemurs on the island. This could be done in all seasons allowing for a more detailed analysis that could identify significant differences between diets. This would also further determine the foraging effects due to the loss of redbay. An analysis of preference for nutrient content should also be conducted because amount of provisions has changed since studies such as this were last conducted. Population density has changed from past studies and could be affecting competition for resources. This should be studied in order to assess if competition for food resources has

increased and if any differences in foraging behavior results from this increase in competition. To further test the effect of provisions on natural foraging, an experiment should be conducted with provisioning removed for a couple weeks. This would allow for a clearer relationship between these two factors, which would be beneficial for management on St. Catherine's Island and any future translocations. By understanding how much foraging on specific food types and species would increase or change because of lack of provisions would be highly beneficial and provide more information on how to introduce ring-tailed lemurs. Also by removing provisioning in this population, female dominance behavior could be studied in this setting and if they would express their dominance in a natural foraging setting. Provision use in winter needs to be further studied to determine if lemurs do rely less on this resource in winter as my results suggested. If the population does not need it, then it can be reduced or not given thus saving managers' money. My study has provided more information about the complex relationship between female dominance, provision use, and natural foraging, which must be taken into account during management of translocated populations of ring-tailed lemurs.

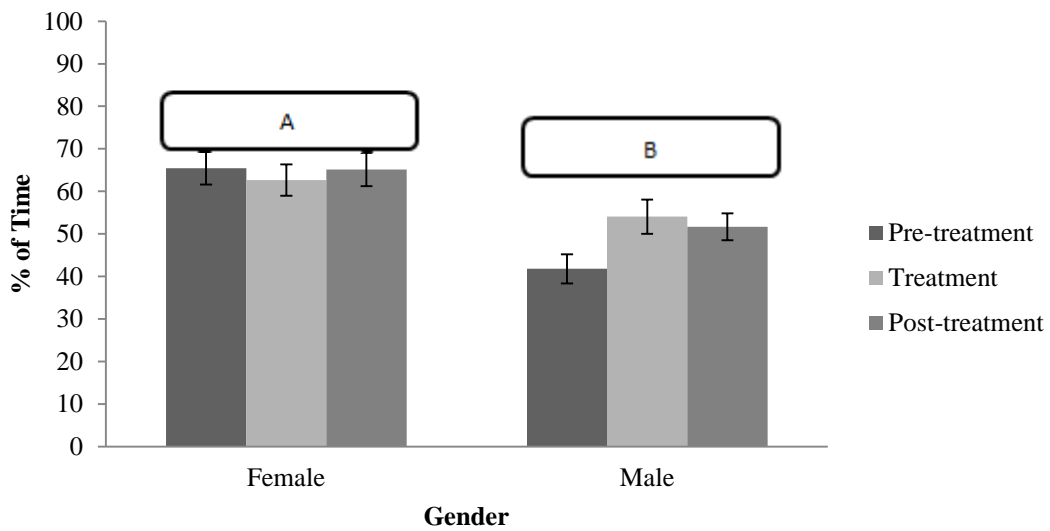


Figure 1. Percent of time spent consuming provisions in males and females is shown for all three phases (± 1 SE). Differing letters indicate significance. Females spend significant more time consuming provisions overall than males ($p < 0.05$; Table 3). Phase did not change time spent at provision sites for either gender (Table 3).

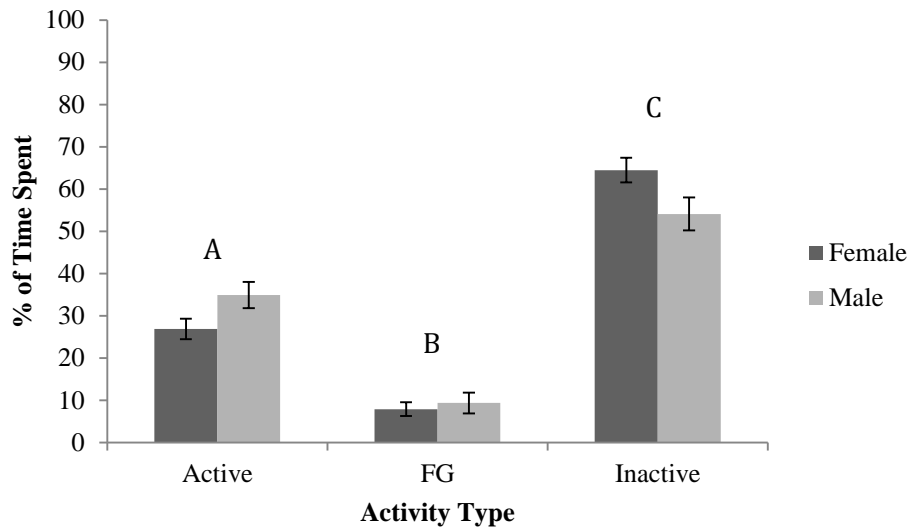


Figure 2. Differences in percent of time spent engaging in active, foraging (FG) and inactive behaviors are shown for both genders (± 1 SE) for pre-treatment phase. Differing letters denote significance. All three activity types are significantly different from each other (Table 4).

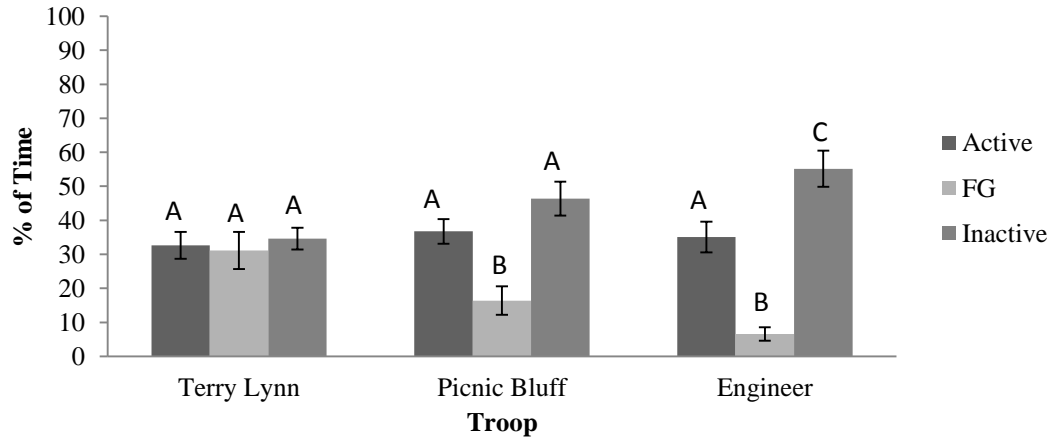


Figure 3. Percent of time spent in each activity is shown for each of the three troops observed in winter (± 1 SE). Differing letters indicate significance. Terry Lynn had no difference between activity types (Table 8). A significantly higher percent of time was spent active and inactive than foraging in Picnic Bluff troop (Table 8). Activity type in engineer troop was different for all three activity types (Table 8).

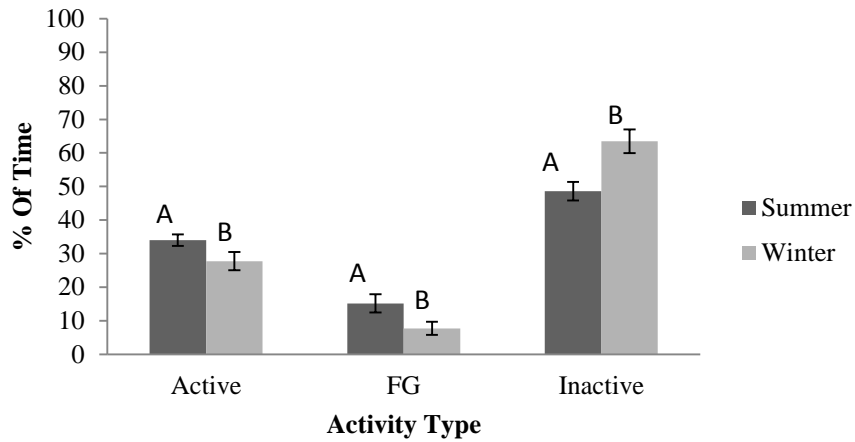


Figure 4. Percent of time spent in each activity type across season is shown for males and females combined (± 1 SE). Different letters indicate significance. A higher percent of time was spent active in summer than winter. More time was spent foraging in summer. Winter had more time spent inactive (Table 8).

Table 1. Age and sex ratios for troops of ring-tailed lemurs observed in this study (Summer 2011).

Troop	# of Males	# of Females	Total #	Adult Females	Adult Males	Subadult Females	Subadult Male
Terry Lynn	1	2	3	1	1	1	0
East Road	2	4	6	3	2	1	0
Engineer	2	4	6	3	1	1	1
Picnic Bluff	3	3	6	3	2	0	1

Table 2. Age and sex ratios for troops of ring-tailed lemurs observed in this study (Winter 2012).

Troop	# of Males	# of Females	Total #	Adult Female	Adult Male	Subadult Females	Subadult Male
Terry Lynn	1	2	3	1	1	1	0
Engineer	1	4	5	3	1	1	0
Picnic Bluff	2	3	5	3	1	0	1

Table 3. Analysis of percent of time spent at provision sites in summer. Percent means \pm 1 SE are shown. F=females, M=males. Pre-treatment, treatment, and post-treatment are indicated by pre, trt, and post respectively. Asterisk (*) indicates significance. Tests used were blocked ANOVAs.

Provision Use		Mean % \pm 1 SE			F-Ratio	P-value	Df
Pre-treatment Gender by Half	gender	F: 65.5 \pm 4.5	M: 41.8 \pm 4.9		20.4794	<.0001*	1, 35
	interaction	F 1st: 79.9 \pm 3.3	M 1st: 51.7 \pm 7.3		1.2156	NS	1, 35
		F 2nd: 51.0 \pm 6.2	M 2nd: 32.0 \pm 4.5				
Half	1st: 69.1 \pm 4.5	2nd: 43.8 \pm 4.6		23.3209	<.0001*	1, 35	
Treatment Gender by Half	gender	F: 63.9 \pm 5.3	M: 53.2 \pm 5.7		4.017	0.0528	1, 35
	interaction	F 1st: 84.4 \pm 3.3	M 1 st : 63.8 \pm 4.8		3.1743	0.0835	1, 35
		F 2nd: 43.4 \pm 6.0	M 2nd: 42.6 \pm 9.2				
Half	1st: 76.6 \pm 3.5	2nd: 43.1 \pm 5.0		26.1895	<.0001*	1, 35	
Post-treatment Gender by Half	gender	F: 65.1 \pm 5.2	M: 51.7 \pm 4.8		6.2735	0.0171*	1, 35
	interaction	F 1st: 82.4 \pm 5.1	M 1st: 58.7 \pm 6.3		4.0185	0.0528	1, 35
		F 2nd: 47.9 \pm 6.3	M 2nd: 44.7 \pm 6.7				
Half	1st: 73.3 \pm 4.6	2nd: 46.7 \pm 4.6		18.4661	0.0001*	1, 35	
Across Phases Gender by Phase	gender	F: 64.4 \pm 2.2	M: 49.2 \pm 2.3		24.6353	<.0001*	1, 54
	interaction	F Pre: 65.4 \pm 3.8	F Trt: 62.6 \pm 3.7	F Post: 65.1 \pm 3.9	2.0787	NS	2, 54
		M Pre: 41.8 \pm 3.4	M Trt: 54.1 \pm 4.0	M Post: 51.7 \pm 3.2			
Phase	Pre: 56.4 \pm 3.7	Trt: 59.4 \pm 2.8	Post: 60.0 \pm 3.0		1.0381	NS	2, 54

Table 4. Analysis of activity type within pre-treatment phase and across phases is shown. Percent mean \pm 1 SE is reported. Active(A) indicates all active non-foraging behaviors. Inactive (I) indicates inactive behaviors (sitting and sleeping). Forage (FG) indicates foraging behaviors. Asterisk (*) indicates significance. Tests used were two-way and repeated measures ANOVAs.

Activity Type		Mean % \pm 1 SE			F-ratio	P-value	Df
Pre-treatment	Activity	Female A: 26.9 \pm 2.4	Female FG: 7.9 \pm 1.6	Female I: 64.5 \pm 2.9	142.1173	<0.0001*	2,57
	Interaction	Male A: 34.9 \pm 3.1	Male FG: 9.4 \pm 2.5	Male I: 54.1 \pm 3.9	4.0518	0.0226*	2,57
Across Phases		Pre-treatment	Treatment	Post-treatment			
Females	Active	26.9 \pm 2.4	33.6 \pm 3.7	30.7 \pm 3.1	1.1254	NS	2,36
	FG	7.9 \pm 1.6	5.2 \pm 1.0	7.5 \pm 1.4	0.9409	NS	2,36
	Inactive	64.5 \pm 2.9	60.5 \pm 4.4	61.5 \pm 3.3	0.3266	NS	2,36
Males	Active	34.9 \pm 3.1	38.2 \pm 3.6	47.0 \pm 5.4	2.2567	NS	2,21
	FG	9.4 \pm 2.5	8.6 \pm 1.2	8.4 \pm 2.0	0.1033	NS	2,21
	Inactive	54.1 \pm 3.9	53.2 \pm 3.0	44.2 \pm 4.7	2.0195	NS	2,21

Table 5. Analysis for food type within phase is shown. Mean percent of time \pm 1 SE is reported. Asterisk (*) indicates significance.

Miscellaneous items consisted of pine cones, pollen part, unknown, stem, bark, and flower. ET represents leftover provisions. Tests used were two way ANOVAs (pre-treatment and treatment) and Scherer-Ray-Hare test (post-treatment).

Food Type		Mean % \pm 1 SE						F-ratio	P-value	df
		Acorns	Soil	ET	Fruit	Leaf	Misc			
Pre-treatment	food type:	23.6 \pm 6.6	5.0 \pm 1.8	21.6 \pm 6.4	16.6 \pm 10.1	10.0 \pm 6.2	23.6 \pm 8.2	1.5245	NS	5,36
	interaction							0.997	NS	5,36
Treatment	food type:	14.3 \pm 6.8	11.2 \pm 4.9	45.1 \pm 12.0		18.8 \pm 8.9	10.6 \pm 5.0	2.6936	0.0498*	4,30
	interaction							1.1789	NS	4,30
Post-treatment	food type:	16.4 \pm 5.9	3.2 \pm 1.3	30.6 \pm 5.7	27.2 \pm 6.9	13.4 \pm 7.4	9.2 \pm 2.9	H=3.55	x ² =11.07	5,30
	interaction							H=1.43	x ² =11.07	5,30

Table 6. Analysis of plant species consumed within phase is shown. Percent mean \pm 1 SE is reported. Asterisk (*) indicates significance. *Quercus*, *Vitis*, *Morella*, *Vaccinium*, and Unknown are represented by Q, Vi, M, Va, and U respectively. Test used was two-way ANOVA.

Plant Species		Mean % \pm 1 SE				F-ratio	P-value	Df
Pre-treatment	Species	Q: 61.1 \pm 13.3	Vi: 20.9 \pm 10.3			4.933	0.0464*	1,12
	Interaction				0.841	NS	1,12	
Treatment	Species	Q: 72.1 \pm 16.1	Vi: 2.7 \pm 1.7	M: 5.4 \pm 5.4		9.6019	0.0032*	2,12
	Interaction				0.23	NS	2,12	
Post-treatment	Species	Q: 39.1 \pm 8.9	Vi: 41.3 \pm 10.8	Va: 4.5 \pm 4.3	U: 6.7 \pm 4.1	6.7946	0.0018*	3,24
	Interaction					0.2651	NS	3,24

Table 7. Significance of time spent consuming provisioning is shown across seasons. Only Engineer and Picnic Bluff troops were used in analysis. Asterisk (*) represents significance ($p < 0.05$). Means given as percent of time spent \pm 1SE. Females and males signified by F and M respectively. Test was blocked two way ANOVA.

Provision Use		Mean % \pm 1 SE		F-ratio	P-value	Df
Across Season	season:	Summer: 60.7 \pm 5.0	Winter: 49.7 \pm 6.5	4.0457	0.0626	1,15
	gender:	F: 62.2 \pm 4.0	M: 38.8 \pm 6.9	3.6346	0.0068*	1,5
Gender by Season	interaction:	F Summer: 67.7 \pm 4.7	F Winter: 56.7 \pm 6.2	2.0101	NS	1,15
		M Summer: 44.4 \pm 5.2	M Winter: 33.2 \pm 13.5			

Table 8. Percent of time spent in activity patterns across a number of variables. Means are reported as percent of time spent \pm 1 SE.

A=Active, FG=Foraging, I=Inactive. Asterisk (*) denotes significance. Tests run were two-, one-way ANOVAs and repeated measure.

Activity Type		Mean % \pm 1 SE			F-ratio	P-value	Df
Summer	activity type:	Female A: 26.9 \pm 2.4	Female FG: 7.9 \pm 1.6	Female I: 64.5 \pm 2.9	142.1173	<0.0001*	2,57
	interaction:	Male A: 34.9 \pm 3.1	Male FG: 9.4 \pm 2.5	Male I: 54.1 \pm 3.9	4.0518	0.0226*	2,57
Winter	activity type:	A: 34.0 \pm 1.7	FG: 15.2 \pm 2.7	I: 48.6 \pm 2.7	36.564	<0.0001*	2,33
	interaction:				0.1822	NS	2,33
Across Season	active:	Summer: 34.0 \pm 1.7	Winter: 27.8 \pm 2.7		5.0395	0.0347*	1,23
	foraging:	Summer: 15.2 \pm 2.7	Winter: 7.8 \pm 2.0		5.734	0.0252*	1,23
	inactive:	Summer: 48.6 \pm 2.7	Winter: 63.5 \pm 3.5		11.9463	0.0021*	1,23
Overall Gender Comparison	active:	Female: 28.5 \pm 1.9	Male: 36.3 \pm 2.8		5.9228	0.0231*	1,23
	foraging:	Female: 11.4 \pm 2.0	Male: 11.7 \pm 4.1		0.0018	NS	1,23
	inactive:	Female: 58.3 \pm 3.4	Male: 50.9 \pm 3.8		2.4955	NS	1,23
Across Season Females	active:	Summer: 33.1 \pm 1.5	Winter: 24.0 \pm 2.7		8.7571	0.0092*	1,16
	foraging:	Summer: 15.3 \pm 2.8	Winter: 7.4 \pm 2.3		5.6973	0.0297*	1,16
	inactive:	Summer: 48.8 \pm 3.8	Winter: 67.8 \pm 3.3		14.4082	0.0016*	1,16
Across Season Males	active:	Summer: 36.3 \pm 4.7	Winter: 36.3 \pm 3.9		0.0002	NS	1,6
	foraging:	Summer: 14.9 \pm 7.1	Winter: 8.5 \pm 4.4		0.6515	NS	1,6
	inactive:	Summer: 48.1 \pm 3.5	Winter: 53.7 \pm 7		0.5107	NS	1,6
Terry Lynn	Summer	A: 27.1 \pm 6.9	FG: 6.7 \pm 1.1	I: 65.0 \pm 13.5	11.7143	0.0382*	2,3
	Winter	A: 35.2 \pm 5.1	FG: 30.6 \pm 2.5	I: 33.8 \pm 2.1	0.4296	NS	2,6
Picnic Bluff	Summer	A: 29.7 \pm 5.6	FG: 10.8 \pm 4.1	I: 57.8 \pm 6.9	23.8891	0.0003*	2,9
	Winter	A: 33.0 \pm 2.0	FG: 12.4 \pm 1.7	I: 54.1 \pm 1.9	107.1879	<0.0001*	2,9
Engineer	Summer	A: 26.2 \pm 3.1	FG: 5.3 \pm 3.0	I: 68.2 \pm 4.1	29.6426	0.0001	2,9
	Winter	A: 34.4 \pm 3.3	FG: 8.7 \pm 2.3	I: 51.9 \pm 3.3	58.8447	<0.0001*	2,9

Table 9. Analysis of percent of time spent consuming food types is shown within both seasons. Percent means \pm 1 SE are shown.

Miscellaneous items consisted of pine cones, pollen part, unknown, stem, bark, and flower. Asterisk (*) denotes significance. Tests used were two-way ANOVAs.

Food Type		Mean % \pm 1 SE						F-ratio	P-value	Df
		Acorns	Soil	ET	Fruit	Leaf	Misc			
Summer	food type:	23.6 \pm 6.6	5.0 \pm 1.8	21.6 \pm 6.4	16.6 \pm 10.1	9.6 \pm 6.2	23.6 \pm 8.2	1.5245	NS	5,36
	interaction							0.997	NS	5,36
Winter	food type:	44.9 \pm 3.0		5.9 \pm 4.0	15.1 \pm 5.7	22.5 \pm 8.6	11.5 \pm 5.3	4.453	0.0098*	4,20
	interaction							0.2101	NS	4,20

Table 10. Analysis of food types across season for females is shown. Percent means are given \pm 1 SE. Asterisk (*) indicates significance. Miscellaneous items consisted of pine cones, pollen part, unknown, stem, bark, and flower. Degrees of freedom were one and four. Tests used were repeated measures.

Females Food Type	Mean % \pm 1 SE		F-value	P-value
	Summer	Winter		
Acorns	39.7 \pm 22.2	22.8 \pm 11.6	1.8714	0.2431
Soil	3.2 \pm 1.8	1.5 \pm 1.4	124.3565	0.0004*
Leftover Provisions	21.8 \pm 13.4	21.6 \pm 7.5	1.0475	0.3639
Fruit	7.5 \pm 7.5	27.2 \pm 27.2	0.2609	0.6364
Leaf	3.1 \pm 2.1	8.2 \pm 5.9	6.2949	0.0661
Misc	24.7 \pm 22.5	18.6 \pm 12.8	1.3741	0.3062

Table 11. Analysis of food types across season for males is shown. Percent means are given ± 1 SE. Asterisk (*) indicates significance. Miscellaneous items consisted of pine cones, pollen part, unknown, stem, bark, and flower. Degrees of freedom were one and four. Tests used were repeated measures.

Males Food Type	Mean % ± 1 SE		F-value	P-value
	Summer	Winter		
Acorns	47.4 \pm 3.5	42.5 \pm 5.1	0.2428	0.648
Soil	0 \pm 0	0.7 \pm 0.7	0.3927	0.5649
Leftover Provisions	8.1 \pm 7.9	3.7 \pm 3.7	6.4337	0.0642
Fruit	3.7 \pm 3.7	26.5 \pm 4.0	0	0.9984
Leaf	36.0 \pm 12.9	8.9 \pm 4.5	0.3245	0.5994
Misc	5.3 \pm 4.5	17.7 \pm 8.9	0.0161	0.9051

Table 12. Analysis of plant species within season is shown. Percent means reported with ± 1 SE. *Quercus*, *Vitis*, *Morella*, and *Sabal* are represented by Q, Vi, M, and S respectively. Tests used were two-way ANOVAs.

Plant Species		Mean % ± 1 SE			F-ratio	p-value	Df
Summer	species:	Q: 61.1 \pm 13.3	Vi: 20.9 \pm 10.3		4.933	0.0464*	1,12
	Interaction				0.841	0.841	1,12
Winter	species:	Q: 63.1 \pm 4.5	M: 15.4 \pm 8.8	S: 14.0 \pm 5.4	13.4608	0.0009*	2,12
	Interaction				0.2631	0.773	2,12

Table 13. Comparison of plant species foraged on by ring-tailed lemurs in five studies conducted on St. Catherine's Island. Studies used in this comparison are Keith-Lucas et al. (1999), Dierenfeld and McCann (1999), Savage (2005), Coleman (2007), and my study. Species foraged upon are indicated by an X.

Plant Species	Keith-Lucas et al	Dierenfeld and McCann	Savage	Coleman	My Study
<i>Acer rubrum</i>			X	X	
<i>Arundinaria gigantea</i>		X			X
<i>Bumelia tena</i>		X		X	
<i>Carya ovalis</i>	X	X			
<i>Celtis</i> spp.	X	X			
<i>Chenopodium ambrosioides</i>	X	X			
<i>Cornus florida</i>	X	X			
<i>Diospyros virginiana</i>		X		X	
<i>Ficus</i>	X				
<i>Helianthemum corymbosum</i>				X	
<i>Ilex</i> spp.		X	X	X	
<i>Juniperus silicid</i>		X			
<i>Liquidambar styraciflua</i>					X
<i>Lyonia ligustrina</i>				X	
<i>Magnolia grandiflora</i>	X	X	X	X	
<i>Melia azedarach</i>	X	X	X		
<i>Mikania scandens</i>				X	
<i>Morus</i> spp.	X				
<i>Morella cerifera</i>	X	X	X	X	X
<i>Nyssa sylvatica</i>				X	
<i>Parthenocissus quinquefolia</i>		X			
<i>Persea borbonia</i>	X	X	X	X	
<i>Phoradendron flavescens</i>		X	X	X	
<i>Pinus</i> spp.	X	X		X	X
<i>Pleopeltis polypodioides</i>			X	X	
<i>Prunus caroliniana</i>	X	X	X		
<i>Pterocaulon pycnostachyum</i>			X	X	X
<i>Quercus</i> spp.	X	X	X	X	X
<i>Rubus betuifolius</i>		X			
<i>Sassafras albidum</i>			X		
<i>Sabal palmetto</i>	X	X	X	X	X

Table 13. (continued)

<i>Saururus cernuus</i>				X	
<i>Serenoa repens</i>			X		
<i>Smilax</i> spp.		X	X	X	
<i>Solanum nigrum</i>		X			
<i>Tillandsia usneoides</i>		X	X	X	X
<i>Toxicodendron radicans</i>			X	X	
<i>Vaccinium arboretum</i>	X	X	X	X	X
<i>Vitis</i> spp.	X	X	X	X	X
<i>Zanthoxylum clava-herculis</i>		X	X		
Total	16	26	20	23	10

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