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Home Range and Provisioning Use of Semi-Free-Ranging Ringtailed Lemurs (Lemur Catta)

Jennifer Ann Savage

HOME RANGE AND PROVISIONING USE OF SEMI-FREE-RANGING RINGTAILED LEMURS (*LEMUR CATTA*)

by

JENNIFER ANN SAVAGE

(Under the Direction of C. Ray Chandler)

ABSTRACT

The ringtailed lemur (*Lemur catta*) population on St. Catherines Island (SCI) may serve as a model system for reintroduction. Free-ranging troops of ringtailed lemurs have been managed on SCI since 1985 and are monitored and provisioned daily. There has been no assessment of the effects of provisioning or seasonal dependence on provisioning to date. Ringtailed lemur troop home ranges and use of provisions were quantified to examine seasonal patterns and changes in relation to habitat quality of the home range. Activity, ranging behavior, and provisioning use were monitored for one year. Habitat assessment of forage species was conducted through stratified random sampling in each home range. There was significant variation among troops in the amount of provisions consumed and significant variation in amount of provisions consumed across seasons. Home ranges varied in size significantly among troops but not across seasons. Choice of natural forage varied across seasons. There was no relationship between habitat quality and home range size or use of provisions. These data suggest that provisioning ringtailed lemurs on St. Catherines Island does not appear to inhibit natural foraging and ranging behavior. This study provides useful information for managing, reintroducing or translocating troops of ringtailed lemurs.

INDEX WORDS: Ringtailed lemurs, *Lemur catta*, home range, provisioning use, habitat quality, reintroduction

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RINGTAILED LEMURS (*LEMUR CATTA*)

by

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DEDICATION

This thesis is dedicated to my father and mother. Thank you for believing in me and encouraging me to keep growing and learning in everything I do.

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CHAPTER 1

INTRODUCTION

We are in the midst of what some have called a “biodiversity crisis.” According to the United Nations Environmental Program, the current extinction rate may be up to 1000 times faster it would naturally be (Heywood 1995), and it is estimated that we are losing approximately 137 species each day (Wilson 1992, Heywood 1995). In response to this crisis, several innovative techniques have been developed to intervene on the behalf of endangered species and the ecosystems that support them. *In situ* efforts include the regulation of biological resources, promotion of sustainable development, habitat protection and rehabilitation, prevention of introduction of alien species, and research on the biodiversity and ecology of fragile systems. To support conservation endeavors in the wild, conservation organizations around the world also work to preserve species *ex situ*. *Ex situ* management of a species is an attempt to preserve genetic diversity and viability of populations in a captive setting, and it includes captive breeding and integrated management through translocation, reintroduction, and re-stocking (International Union for the Conservation of Nature [IUCN] 2002).

Captive breeding often involves exhibiting species in zoos and botanical gardens. These institutions provide a critical connection to *in situ* conservation through education and promotion of conservation issues. Many zoos and botanical gardens support *in situ* programs financially and through a variety of research initiatives. In zoos, captive components of populations are employed as surrogates for wild animals in endangered species research (Conway 1995). Zoos work cooperatively to maintain genetic diversity of populations, develop programs for species survival, and link captive programs with *in* *situ* conservation efforts. To establish a link between *ex situ* and *in situ* efforts, captive breeding must focus on species with realistic prospects for reintroduction (Blamford et al. 1996). Captive breeding aimed at reintroduction can help to restore ecosystems and, potentially, successful reintroduction frees zoo space for additional taxa (Blamford et al. 1996). More than half of the reintroduction projects surveyed used zoo-bred animals or the captive-bred descendants of zoo animals (Beck et al. 1994). Nearly all of the founders of the release populations of the Golden lion tamarin (*Leontopithecus rosalia*), North American red wolf (*Canis rufus*), and the Arabian oryx (*Oryx leucoryx*) were born and raised in zoos (Beck et al. 1991).

The candidates for reintroduction or re-stocking (see IUCN 1987, Kleiman 1989, Kleiman et al. 1994 for detailed definition of terms related to reintroduction) may be either small native populations or captive-bred animals that could be used for release in protected habitats. Sufficient stock from viable self-sustaining, well-managed, captive populations that possess the genetic diversity and physical capability for reintroduction should only be considered (Konstant and Mittermeier 1982, Kleiman 1989, Kleiman et al. 1994). Several conditions must be met to achieve the goals set by the IUCN for successful reintroductions. These conditions include eliminating the causes of decline of the species, enforcing protection of habitats and preserves that contain them, and determining release protocols that ensure the viability of released animals (Brambell, 1977, Konstant and Mittermeier 1982, Kleiman, 1989, Chivers 1991, Kleiman et al. 1994).

Kleiman (1989) emphasizes two critical factors that contribute to the success of a release. These are feasibility studies of the demography and behavioral ecology of the species and pre- and post-release training for the release animals. Training is species-specific. In the case of arboreal primates, they must be trained in predator avoidance, the ability to find and process food, interaction with conspecifics, building shelters and nests, and — possibly most importantly— orientation and navigation in a complex terrain (Kleiman 1989). In order to identify species-specific needs and direct the focus of training, an important prerequisite to the reintroduction of primates is research on the habitat, home range, foraging behavior, and shelter needs of the species involved.

Pre- and post-release training usually involves a period of “soft-release,” which aids in the animals’ adjustment to new terrain. This is necessary because captive environments may not have the structural complexity of natural environments, and this shortcoming may prevent an arboreal primate from developing the skills necessary to face the challenges associated with feeding the wild (Britt 1998). Animals raised in captivity have predictable perching and resting platforms and regular, dependable provisions. Britt (1998) suggested that placing animals in a spatially complex and naturally stimulating environment could encourage feeding skills necessary for the wild. Soft-release programs gradually transition animals from a routine, captive environment to a full release. In order to ease this progression, animals are continually provisioned with food and allowed out of their cages for progressively longer periods until it is determined that they are capable of navigating their new terrain, at which point they can be monitored and studied to examine their adjustment to a new environment. Full release can be achieved once the captive population is transitioned to a free-ranging situation where it can sustain itself with minimal or no intervention.

Efforts to reintroduce, translocate, and introduce primates have largely been focused in the New World. The golden lion tamarin reintroduction in Brazil is probably the most publicized primate reintroduction to date. This program has been criticized for its variable success and cost (Kleiman et al. 1991). Both trained and untrained tamarins were part of the release group. Pre-release training of captive-born golden lion tamarins involved allowing animals to range throughout zoo grounds and presenting their food in feeders that required manual probing, such as puzzle boxes that forced animals to search and extract food (Kleiman 1989,Stoinski et al. 2002). Although pre-release training did not significantly affect survival after release, it has been suggested that the duration of training was insufficient (Beck et al. 2002, Stoinski et al. 2002). Pre-release training for these individuals only took place for a period of six months. Stoinski et al. (2002) suggest that acclimatization in locomotor skills can take at least one year and, more likely, up to two years. This was evidenced by the fact that captive-born, first-generation and second-generation animals differed significantly in their locomotor skills (Stoinski et al. 2002). Captive-born animals spent significantly more time on substrates 2-5 cm in diameter, human-made substrates, and the ground. They also rested less and fell more than their first-generation, wild-born offspring (Stoinski et al. 2002). In addition to poor locomotor skills, captive-born individuals lacked foraging skills. Captive-born animals were observed to wait for food instead of actively searching for it, and therefore exhausted nearby resources (Stoinski et al. 2002). Pre-release training only provided a short-term advantage, but post-release training in the form of provisioned food, water, and shelter has been identified as increasing the survivorship of reintroduced animals and as a more effective use of resources of time, labor, and expenses (Kleiman et al. 1991, Beck et al. 2002).

It has been suggested that the availability of reliable food can diminish stress associated with reintroduction and smooth the transition to independent foraging (Konstant and Mittermeier 1982). However, dependence on provisioning is not well studied. The reintroduction of the Panamanian black-handed spider monkey (*Ateles geoffroyi panamensis*) on Barro Colorado Island, Panama was considered successful (Konstant and Mittermeier 1982). However, this success was probably due to access to additional food and shelter and the lack of conspecifics in the area (Konstant and Mittermeier 1982). Animals that were released in the laboratory clearing area remained in close proximity to this region. This region remained part of the spider monkey's core area, or area of maximum use, and it was suggested that although they were not deliberately provisioned, they had access to non-offered food and shelter in this region (Dare 1974). Animals released on other parts of the island, or those that left the research compound, apparently did not survive (Dare 1974).

Provisioning may be beneficial in the short-term, but it can also inhibit natural daily movements and foraging as in the golden lion tamarin (Stoinski et al. 2002). Provisioning may be maladaptive in long-term management plans aimed at maximizing natural adaptive processes (Tear and Ables 1999, Stoinski et al. 2002). In the case of the Arabian oryx, supplemental food and water were provided post-release to minimize the challenges of naturally varying environmental conditions (Tear and Ables 1999). However, this enabled herds to live at higher densities near an artificial food supply. Tear and Ables (1999) indicate that this presents a management dilemma in that the benefits of short-term aid such as provisioning may delay the development of adaptive behaviors needed for long-term success.

There is a need to determine the effects of provisioning wild, reintroduced, and translocated animals. Ostensibly, provisions should benefit introduced or translocated individuals by assisting in their transition to their new surroundings and by providing a reliable food source when natural forage is unpredictable or unavailable seasonally. However, it also may reduce spatial movements or inhibit the development of species-specific behaviors such as feeding postures necessary for extracting food in trees and climbing and agility skills for moving throughout the forest on pliable and unpredictable substrates such as tree limbs and vines. Provisioning may be necessary to acclimate released animals but it is not known how long this assistance is necessary and if it could eventually be detrimental to their ability to develop natural foraging skills necessary for survival. Provisioning may be critical for some species when resources are seasonally poor, and it may be unnecessary in time of seasonal abundance. It may be the case that provisioning is necessary for minimal time period, but to achieve full release of a group of captive-bred animals, provisioning may need to be progressively discontinued so that natural behaviors can take hold.

The purpose of this thesis was to examine a model of reintroduction of captive-bred primates with an emphasis on the interplay between provisioning and activities away from the provisioning area, such as foraging and activity budgets. In addition, I examined the role of provisioning as a captive management tool to determine if it is necessary once animals have been successfully transitioned to a full release situation. Provisioning budgets can be expensive for zoos and release programs. The degree to which released animals depend on provisioning may not be consistent or even necessary should their adjustment to natural resources prove to be sufficient. However, resource abundance can be seasonal and, in turn, dependence on provisioning can vary with resource availability. Once dependence on provisioning can be quantified, I may be able to show that provisioning can be minimized or varied throughout the year. This could potentially save captive managers and release biologists much needed money that could be spent on other conservation efforts. My research focuses on a model system, the captive management of a small population of primates that could be considered reintroduction candidates, the ringtailed lemur (*Lemur catta*).

Study Species

The ringtailed lemur, with a population between 10,000 and 100,000 individuals, is a small Prosimian primate that occupies the dry southern region of Madagascar (Mittermeier et al. 1992). The IUCN categorizes the degree of biological threat for this species as High Priority, and the IUCN listed ringtailed lemurs as vulnerable in 2004 (IUCN 2004). Vulnerable is defined by the IUCN (2004) as animals that are facing a high risk of extinction in the wild in the medium-term future due to an observed, inferred, or suspected reduction of their population of at least 20% over the next 10 years or three generations, whichever is longer. The reduction in the population is based on the decline in area occupancy, extent of occurrence, and/or quality of habitat (IUCN 2004). In 1992, satellite surveys of Madagascar revealed that *Lemur catta* habitat— dry scrub and closed canopy forest— is disappearing rapidly (Mittermeier et al. 1992). Sussman and Green (2003) completed a survey of ringtailed lemur habitat and found that in 1985, only 34% of the estimated original rain forest remained and that it was being cleared at a rate of

110,000 ha/year. Ringtailed lemur groups range in size from 5 – 27 animals, averaging between 13 to 15 individuals (Sussman 1992). A female dominance hierarchy characterizes groups that consist of adult females, their young, central or core males, and peripheral males (Sauther 1991). Ringtailed lemurs are the most commonly found lemur in zoos and probably the most studied of all lemurs (Mittermeier et al. 1992).

Ringtailed lemur territories can vary greatly in size. The Berenty Reserve in Madagascar is a 100-hectare forest that contains ringtailed lemurs and has been extensively studied. Ringtailed lemur troops have been shown to have home ranges from 5.7 hectares (Jolly 1966) to 23 hectares (Budnitz and Dainis 1975). Jolly (1972) and Sussman (1974) observed that wild ringtailed lemur troop territories have extensive overlap. Ringtailed lemurs defend the boundaries of their home range and scent mark more frequently in areas where troops overlap, suggesting that scent marking is a means of intergroup communication (Mertl-Millhollen et. al 1979, Mertl-Millhollen 1988, Kappeler 1998). However, troops will generally avoid each other in these overlapping ranges (Jolly 1972). Mertl-Millhollen (1988) defined ringtailed lemur home range as including any area visited by the troop on more than one occasion. She found that each home range was divided into a core area, used exclusively by that troop, and a surrounding area that overlapped with home ranges of adjacent troops. Ringtailed lemur home range areas can be maintained for extensive periods. Troops in Berenty Reserve, Madagascar maintained continuity in the core area of their range for several years and some troop ranges remained stable for up to 30 years (Jolly et. al 1982, Jolly and Pride 1999).

It has been suggested that territory boundaries tend to show stability, and it seems likely that use depends more on general vegetation pattern than on particular fruiting species or even on the availability of food or cover (Klopfer and Jolly 1970). Budnitz and Dainis (1975) suggest that home range size is related to environmental quality. Studying two wild troops of ringtailed lemurs in a gallery forest, they found that habitat differences between troops were largely based on the concentration of tamarind trees, a primary food resource for *Lemur catta*. A lemur troop with closed canopy characterized by approximately 50 % of ground cover shaded by tamarind trees had roughly one-third of the home range size of a troop with open canopy, brush and scrub habitat with widely dispersed and smaller trees. This second troop traveled longer distances to gain access to their less densely distributed food supply. It has been suggested that ringtailed lemurs can live in large home ranges with patchy food distributions by eating small amounts of many different plant species (Ganzhorn 1986, Sussman 1974). Sussman (1991) and Budnitz (1978) indicated that population density and home range sizes of ringtailed lemurs vary based on forest type. Sussman (1991) suggested that ringtailed lemurs that live in the dry portion of the forest would need home ranges of about 37 ha to have the same number of trees as ringtailed lemurs that live nearer a river with an average home range size equal to 15 ha. Budnitz (1978) found that troops whose home ranges include closed-canopy forest and access to the river have smaller home ranges than troops living in scrubby habitat without access to open water.

Ringtailed lemurs are sensitive to changes in their food supply, and seasonal variation in resources can affect survival. Mertl-Millhollen et al. (2003) investigated the relationship among home range size, food abundance, and environmental stress with pregnant ringtailed lemurs. She found that ringtailed lemur troops selected resources that contained more water and protein, and adjusted their spatial activity to the abundance of resources during stressful periods. The ringtailed lemurs in this study moved to areas with a higher abundance of fruit in a time of environmental and physical stress (Mertl-Millhollen et al. 2003). Sauther (1998) argued that ringtailed lemur conservation is dependent on the presence of lush riverine forests and, in highly seasonal habitats, the loss of ground plant or keystone species can impact their survival. This is evidenced by high maternal mortality in ringtailed lemurs during periods of draught and subsequent changes in the phenology of forage species (Sauther 1998).

St. Catherines Island Ringtailed Population

In 1985, the Wildlife Conservation Society introduced an experimental group of semi-free-ranging ringtailed lemurs on St. Catherines Island (SCI), Liberty County, Georgia. The goal of the release was to explore various aspects of release biology. The release was conducted to examine whether captive-born, caged individuals could develop social and ecological behaviors that resembled the species-typical behaviors of wild and free-ranging animals and to determine if these behaviors varied due to environmental conditions (Keith-Lucas et al. 1999). Another important aspect of releasing captive-born animals was to determine how they interact with conspecifics. Primates form complex social groups and it is important to study how the introduction of strangers can disrupt group structure (Chivers 1991). Subsequent groups of ringtailed lemurs were added on SCI from 1986 through 1991 to study interactions between groups. This population provides a unique research potential for reintroduction and translocation studies in addition to studies of ringtailed lemur social dynamics.

Currently, there are three semi-free-ranging troops ranging in size from 14 to 19 individuals occupying the north end of the island. The ringtailed lemurs on SCI are considered "semi-free-ranging" because they are provisioned daily with commercial monkey chow, fruits, and vegetables. Groups vary in their social structure, activity, apparent home range, and daily travel distance (pers. obs). Studies of lemurs on SCI have largely focused on social behavior (Keith-Lucas et al. 1999; Parga 2002, 2003; Parga and Lessnau, in press). Nutritional needs and foraging behavior of the SCI lemurs have also been assessed. Dierenfeld and McCann (1999) examined the nutrient composition of plant species eaten by SCI lemurs with special interest in the plant, part of plant, and time spent foraging. Dierenfeld and McCann (1999) suggest that provisioning may diminish the need to forage on natural items. Dierenfeld and McCann (1999) considered that in addition to studying foraging time as an essential component to release and reintroduction programs, chemical data on the nutrient resources can be useful in considering habitat for release programs. Mowry et al. (1997) collected samples of non-provisioned food items eaten on SCI and analyzed them for secondary compounds in order to assess their impact on food choice. There are no descriptive plant diversity indices on the different parts of the island that the lemurs inhabit. The ringtailed lemurs on SCI may vary in the ways in which they use their habitat and their activity based on seasonal changes and access to resources. However, their seasonal dependence on provisioning has not yet been quantified (Dierenfeld and McCann 1999).

The goals of this study are to establish the relationship among provisioning use, home range size, and habitat quality of the ringtailed lemurs on SCI. This information will play a valuable role in determining the needs of the semi free-ranging ringtailed lemur population on SCI and will provide insight into aspects of release biology of captive species. This assessment will be useful to those making recommendations for release, translocation, and reintroduction of ringtailed lemurs and possibly other species of small primates. It will establish the baseline provisioning needs of released troops of lemurs on SCI in relation to the release habitat. Ultimately, it is my objective to show how access to provisions relates to troop movement and general activity if the need to forage is diminished through supplemental feeding.

To determine the relationship between provisioning, home range size, and habitat quality, I asked three main questions: 1) Does provisioning use vary among troops of lemurs on SCI? Home ranges that are abundant in flowering trees, fruits, and seeds should be relatively smaller than territories that contain sparse or non-productive vegetation (Budnitz and Dainis 1975). I predicted that troops with better habitat quality in terms of forage resources would use less provisioned food. 2) Does provisioning use vary seasonally? There are periods when the SCI lemurs do not return to their release sites, sometimes for bouts of several days when indigenous fruits and seeds are abundant. This suggests that there may be sufficient resources to sustain the troops without provisioned diets at seasonal periods throughout the year. I predicted that ringtailed lemur troops would use less provisioned food when forage items are abundant. 3) Do home ranges vary in size and is this variation related to provisioning use or habitat quality? The relationship between home range habitat and provisioning may show two patterns. First, if home ranges are influenced primarily by availability of natural forage items, then I predict that home ranges would be smaller if the habitat improves seasonally or among groups with more forage species in their home range habitat. On the other hand, if groups use their provisions more, I predict that their home ranges would be smaller since they are relying more on their provisions and not the availability of forage items. To answer these questions, I quantified general activity budget, seasonal provisioning use, seasonal home range size, and home range habitat composition of this experimental population.

CHAPTER 2

METHODS

Study Site

St. Catherines Island (SCI) is a 2900-ha barrier island located 22 km south of Savannah, Georgia, USA. St. Catherines Island supports a wide variety of habitats including mixed deciduous and evergreen forests, fresh and saltwater marshes, swamps, and open grass pastures (Thomas 1988). The island is semitropical with mean annual rainfall of 126 cm; the highest daily mean temperature is 33º C in July and the lowest is 4º C in January (Keith-Lucas et al. 1999).

The St. Catherines Island Foundation manages the island and oversees all research and conservation efforts that take place (Spratt 1999). The Wildlife Conservation Society (WCS) established an off-site breeding (i.e., away from the Bronx Zoo) facility in 1974 committed to working with rare and endangered species that do not thrive in typical zoo settings (Spratt 1999). WCS maintains several exotic species of mammals, reptiles, and birds on St. Catherines Island at the Wildlife Survival Center. The center provides a unique opportunity to explore breeding and management of these species because it is maintained on a barrier island with no public access.

The survival center breeding programs participate with Species Survival Plans to maximize the genetic diversity of critical species and follow recommendations set by Taxon Advisory Groups and the survival plans. Programs include species that exist nowhere else in captivity in North America (for example the Maleo [*Macrocephalon maleo*], and the Cape Hartebeest [*Acelaphus buselaphus caama*]) and reintroduction programs for the Arabian oryx (*Oryx leucoryx*), the black-and-white ruffed lemur

(*Varecia variegata variegata*) and the Wattled Crane (*Bugeranus carunculatus*). In 1985, WCS supported the release of captive-born ringtailed lemurs on the north end of SCI (Keith-Lucas et al. 1999) to examine aspects of release biology. The location of the release sites was based on proximity to roads and open canopy as a cooperative management decision with the St. Catherines Island Foundation and the Wildlife Survival Center.

Study Population

Zoologists manage several groups of ringtailed lemurs on SCI. Management of the ringtailed lemur troops involves monitoring animal health, behavioral activities, social interactions, and veterinary needs. The SCI ringtailed lemur colony is considered "semi-free-ranging" due to the fact that they are provided with daily provisions sufficient to meet their daily caloric and nutrient requirements and are free to range throughout the island. Managers use provisioning to ensure sighting each troop on a daily basis. However, there are times when troops do not return to their shelter sites, so animals are fitted with radio-collars (Telonics, Inc.). The first troop of lemurs, Troop 1, consisted of captive-born individuals that were brought to SCI in 1985 from the WCS's chief captive breeding facility and public zoological garden, the Bronx Zoo, in New York, USA. The six animals (2 adult males and 4 adult females) were transitioned from captivity progressively and eventually achieved full release from their shelter cages. These animals had no experience foraging or navigating in a novel terrain, and they exhibited limited species-typical behaviors in terms of vocalizations and locomotion abilities (Keith-Lucas et al. 1999). This group eventually developed behaviors typical of the species in the wild (Keith-Lucas et al. 1999). To examine interactions between groups, a second troop of captive-born lemurs was released in 1986. This troop consisted of a pair of adults and their four male offspring. The third troop of lemurs was released in 1994 and consisted of 2 adult females and 2 adult males (Robert Lessnau, pers. comm.). Each group had access to heated shelter and water and was provisioned daily at their release site. Over time, managers have removed males and added unrelated males to maintain genetic diversity as recommended by the Species Survival Plan. In addition, individuals are removed from troops due to injury, death, or, in some cases, when troop members have pushed subordinate lemurs out of the group.

At the onset of this study, four separate troops occupied the north end of SCI and ranged in size from 14 to 19 animals per group (Table 1). WCS managers developed three of the four troops. The fourth troop resulted from a fission of the first release group, Troop 1. In the fall of 2000, four females, descendants of the group's founders, departed the group due to conflict among females. Historically, when an individual is pushed out of the troop, WCS staff would capture the individual and try to place him/her in another institution. However, WCS staff did not intervene in this event, as troop fission has been seen in the wild (Hood and Jolly 1995). The females ranged throughout the north end of the island and eventually established a consistent home range where managers could locate them regularly. A male from the third troop (Group B) joined them later that year, thus forming a fourth troop. WCS managers placed a shelter in the region where this fourth troop settled where animals were given fresh water and provisions daily.

Three of the four troops were chosen for this study, Group A, the second release troop, Group B, the third release troop, and Group C, the troop that resulted from the fission. The initial release group (Troop 1) was excluded due to the fact that it exploited other food resources in the Wildlife Survival Center, such as other captive animals' provisioned food, and that it appeared to rely much less on provisions than the other troops. The study was conducted for one-year beginning in June 2002 and ending in July 2003. June served as a piloting period. I collected behavioral data, which included sampling of activity, location, and provisioning consumption, beginning in July 2002 and concluding in July 2003. I sampled habitat and vegetation from September 2003 through April 2004. Because St. Catherine Island is considered semitropical, all data were grouped into bi-monthly categories instead of arbitrarily defined seasons. I decided to group data into bi-monthly categories for two reasons. First, grouping data into monthly categories did not provide a sufficient amount of information. Secondly, grouping data into larger categories, such as three months, would not accurately represent seasonal differences due to climate. Therefore, each set of data was combined into bi-monthly time periods as follows: June/July, August/September, October/November, December/January, February/March, and April/May.

Behavioral Observations

I quantified lemur behavior from July 2002 through July 2003. Troops were followed 1-2 days per week in either a morning or afternoon cycle for several hours per troop. Troop selection was randomized so that each troop would be followed at a different time period for several days per month. I recorded behavioral data by radio-tracking an individual in the troop to find their location. Once the troop was found, I took a Global Positioning System (GPS) reading to record troop location and began sampling behaviors. I used a combination of focal and instantaneous scan sampling (Altmann 1974). Behavioral scans were 31 minutes in duration because I included minute zero in the scan. I recorded the behavior of a randomly chosen animal at 1-min intervals according to my developed ethogram (Table 2). The ethogram used in the study was developed from Parga (2002), which was based upon those used by Taylor (1986), Gould (1994), and Pereira and Kappeler (1997), which were in turn based upon descriptions by Jolly (1966) and Petter and Charles-Dominique (1979). The ethogram included twelve distinct behaviors that reflect ringtailed lemur activity. For the behavior “Forage” I also recorded plant species and part of plant. I used a timer that would sound every 60 sec to signal it was time to record behavior. I included every adult and juvenile in the troop for random selection of a focal animal. Infants were not included in behavioral sampling. At times, the troops get high into the canopy and it was not possible to identify and continuously follow the focal animal. When this occurred, I switched to scanning a different animal every minute to maintain randomness. I estimated the percent of time that lemurs devoted to each behavior by tallying the number of minutes engaged in each behavior per scan and divided this by the duration of the behavioral scan. These data provided an estimate of the activity budget of the animals. I summarized the behavioral data into bi-monthly categories to determine changes in ringtailed lemur activity budget throughout the seasons and also to compare the behavioral data with home range size, provisioning use, and vegetation composition of the group’s habitat.

Provisioning

I quantified use of provisioned food by measuring the amount of provisioned chow and fruit that was consumed. Specific amounts of food were offered daily to each troop based on the number of animals per troop. Staff weighed the diets to ensure that the appropriate amount was offered per troop and divided the provisions into several bowls set at each troop's shelter site. I weighed the diets again at the end of the day to measure the amount consumed by the troop of that day. From August through January, each animal received 90 g of nutritional chow (HMS Primate Diet) and 100 g of various fruits and vegetables such as bananas, grapes, carrots, and others per day. This calculation (using the program Zootrition) was based on the basal metabolic rate determined for small primates recommended by the Wildlife Conservation Society. Zootrition also calculates nutritional needs for pregnancy and lactation. Diets were adjusted by increasing the amount of nutritional chow in February based on the number of females potentially pregnant and then re-adjusted for lactation needs when a female would give birth. Provisioned diets fluctuated somewhat during the birthing season until it was determined that females without infants were, in fact, not pregnant. Troop size was not constant throughout the study due to the fact that males migrated from troop to troop and in instances when an animal was removed from the troop due to death or injury. Diets varied to match the consistent number of animals per troop.

Weighed diets were placed at each of the ringtailed lemur shelter sites every morning between 09:00-11:00 in feeding platforms designed for this study. Diets were placed on baffled, 2-m platforms to prevent other animals (e.g., raccoons, white-tailed deer) from eating their food. Lemurs could leap onto the platforms. Diets were weighed again between 15:00 and 17:00 three to four days per week. Ring-tailed lemurs are diurnal and are not likely to eat overnight. Female ringtailed lemurs are always dominant to males in terms of feeding order. As males attempt to migrate and integrate into a new troop, they are often chased off from the shelter site. I placed several feeding platforms at each site to minimize competition for food and a peripheral feeding platform at each site for subordinate and peripheral animals that could not or would not feed with the troop.

Deer and raccoons were observed at the release sites. Raccoons were not seen getting onto the feeding platforms during daylight hours throughout the study. I attempted to weigh the food the following morning to determine amount of provisioned consumed over a 24-hour period. I did not include these data in the analysis because I could not reliably say whether or nor raccoons were consuming the provisions overnight. In addition, I was not able to go to the lemur release sites early in the morning on a consistent basis.

I used a control bowl to account for moisture weight loss and gain due to ambient conditions. I set the control bowl on a platform covered by 0.25 in (0.064 cm) wire mesh at Group A’s shelter site. When I weighed the diets again in the afternoon to determine the amount consumed, I also weighed the control bowl to determine any weight loss or gain due to ambient conditions. From this, I calculated the percentage of weight loss or gain for the chow. I subtracted the amount of provisions remaining from the amount offered for that particular day to calculate amount of provisions consumed by the troop on that day. I determined the amount of provisions consumed per animal for each troop by dividing the total amount remaining by the total number of animals in the troop for that particular day. I then multiplied this amount by the percentage weight lost or gained as determined by my control bowl to correct for ambient conditions. I summarized the amount consumed per animal per group into bi-monthly categories to examine seasonal changes in dependence on provisioning.

Home Range Assessment

I quantified home range by compiling GPS readings taken during the behavioral observation scans and by observations of troop locations throughout the year. I recorded the GPS reading at the start and end of each behavioral scan to account for troop movement with a Garmin Etrex Legend handheld unit (Garmin, USA). I recorded the time and date of each GPS point. WSC staff, researchers, and I also recorded the location of troops opportunistically. I used the program Gartrip to export the GPS readings from the Garmin handheld unit into Microsoft Excel. I used the Geographic Information System (GIS) program ArcView GIS 3.2 to create home range polygons for each group using the minimum convex polygon (MCP) method (Stickel 1954). All home range polygons were measured in square meters. I created an annual home range map for each troop by including all of the GPS points per group for the year. I projected annual home ranges of each troop onto a photographic map (USGS) of SCI using ArcGIS 8.1 (Figure 1). The map of SCI is a photographic image with 3-m resolution. In addition to annual home range maps, I created six seasonal home range maps by sorting GPS points into bi-monthly time periods (Appendices A-C). The six seasonal maps show home range size for each bi-monthly time period and reflect all of the GPS locations of the troop for the entire sampling period.

Habitat Quality Assessment

To quantify the vegetation in each home range, I randomly sampled each group's annual home range habitat. I established transects across each home range with stratified random sampling. The exact number and length of transects was dependent on the size of the home range. Group A had 6 transects and 26 sampling points. Group B had 9 transects and 27 sampling points. Group C had 6 transects and 30 sampling points. Each transect line was set 100-m apart and ran in north-south direction. I used a compass and 100-m tape to walk transects lines and sampled at pre-selected random points. To examine the composition and structure of the habitat, I sampled each point using several different methods.

I used a spherical densiometer to measure canopy cover. Standing directly at the sampling point, I took a densiometer reading in each of the four cardinal directions to determine the amount of canopy and averaged these results for each point (Figure 2. I measured ground cover by sampling four 1x1-m plots centered on each sampling point and visually estimated the percent of ground covered by vegetation (Figure 2). I averaged these results to determine percent of ground cover for that point. I described the understory by sampling two 5x5-m plots at each sampling point. Each 5x5-m plot was set perpendicular to transect line north of the sampling point (Figure 2). I recorded species, number, and height of all woody stems (defined as trees and woody-stemmed plants less than 3-m tall) in each 5x5-m plot. Forage species were identified as plants and trees that lemurs were observed eating during this study (Table 3).

To measure tree composition and basal area, I sampled one 10x10-m plot set north and west of each sampling point, perpendicular to the transect line (Figure 2). I measured the diameter at breast height, height, and species of each tree taller than 3m in this sample. From these measurements I calculated the basal area per (100 m^2) for each sampling point habitat. I also determined the basal area for each forage species in each groups' habitat. Cabbage Palm (*Sabal palmetto*) was not included in the basal area assessment due to the inability to measure diameter at breast height accurately.

Analysis

All analyses were done with JMP 4.0 statistical analysis software (SAS Institute, Inc.). I performed repeated measures analysis to compare effects for groups and months. Due to the fact that data were not normally distributed and did not show equal variance, I used Wilcoxon Sum of Ranks to compare the percent of time spent in each behavior per scan for each group and for vegetation measurements among groups. I quantified the correlations between behaviors and home range size, behaviors, and provisioning consumption using Spearman's rank (r_s) correlation. In order to compare habitat measurements with home range size and provisioning use, I used Pearson's R correlation.

CHAPTER 3

RESULTS

Behavioral Observations

I collected approximately 360 hours of behavioral data on three lemur troops. At the start of the study, Group A consisted of 18 animals (4 adult males, 8 adult females, 1juvenile, 2 juvenile females and 3 infants). At the end of the study, Group A consisted of 19 animals (1 additional adult male, 8 adult females, 1 juvenile male, 2 juvenile females, and 3 infants). I collected 240 thirty-minute behavioral samples on Group A. Group B started with 19 animals (5 adult males, 9 adult females, and 6 infants). At the end of the study, Group B consisted of 19 animals (2 adult males, 8 adult females, 3 juvenile males, 3 juvenile females, and 3 infants). I collected 244 thirty-minute behavioral samples on this group. Group C started with 14 animals (4 adult males, 4 adult females, 1 juvenile male, 1 juvenile female, and 4 infants) and ended with 13 animals, (2 adult males, 4 adult females, 4 juvenile females, and 3 infants). I collected 246 thirty-minute behavioral samples on this group.

Free-ranging lemurs on St. Catherines Island spent most of their time (approximately 40-50% of their activity budget) resting in trees and sleeping (Table 4). Feeding also took up about 20% of lemurs' activity budget. About half of this feeding time was devoted to foraging and half to consuming provisioned food (Table 4). Perhaps surprisingly, there was little seasonal variation in behavior. Of the behaviors I quantified, only resting ($F_{5, 10}$ = 7.80, P= 0.003) and locomoting in trees ($F_{5,10}$ =6.87, P= 0.005) varied significantly among months. Lemurs spent the most time resting in trees during the June/July time period and they spent more time locomoting in trees during the

Aug/Sept time period (Figure 3). Despite pronounced differences among groups during certain months (e.g. resting on ground in Jan/Feb or travel in Oct/Nov; Fig. 4), there were no significant differences in behavior among groups across the year ($F_{2,10}$ =3.04, P= 0.09).

A critical question for my research concerns how groups spend their time relative to foraging and consuming provisions. The proportion of time spent consuming provisions varied from a high of 11.9 percent in the Dec/Jan bi-monthly time period to a low of 5.7 percent in the Oct/Nov bi-monthly time period (Table 4). However, there was no significant overall effect of month on time spent consuming provisions ($F_{5, 10}$ = 2.44, P= 0.11). The proportion of time spent foraging on natural foods varied from a high of 19.4 percent in the Oct/Nov bi-monthly time period to a low of 8.4 percent in the Apr/May bi-monthly time period (Table 4). However, variation was sufficiently high that there was again no significant overall effect of month on time spent foraging ($F_{5, 10}$ =2.35, P= 0.12). There was also no significant variation among groups for time spent consuming provisions ($F_{2, 10}$ =0.63, P= 0.55) or for time spent foraging ($F_{2, 10}$ =1.87, P= 0.20; Figure 5).

Although the groups spent similar time consuming provisions and foraging, there was variation among groups in the time they spent foraging on specific food items. Ringtailed lemur troops consumed a variety of forage items. Many of these species were common for all troops. All lemur groups foraged frequently on the buds and leaves (17-18 % of foraging time) of Laurel and Live oak trees (*Quercus laurifolia* and *Q. virginiana*), the acorns from these trees (approximately 10% of foraging time), the berries, stalks, and bark (12-13% of foraging time) of Cabbage palm (*Sabal palmetto*), and muscadine grape (*Vitis rotundifolia*) leaves, grapes, and buds (8-9 % of foraging time; Figure 6). Lemurs consumed parts of pines trees (*Pinus* spp.), wax myrtle (*Myrica cerifera*), and sparkleberry (*Vaccinium arboreum*) approximately 5 percent or less of total foraging time (Figure 6). However, specific choice of forage species varied across troops and across seasons (Figure 6).

Lemurs alternated their choice of forage items throughout the year. Foraging activity peaked during the Oct/Nov bi-monthly time period (Figure 5) when a variety of forage items, such as acorns and cabbage palm parts, were seasonally abundant (Figure 6). These items were eaten approximately 38 percent and 28 percent of foraging time respectively during these months. There was a significant month effect on use of acorns ($F_{5, 10}$ =3.84, P= 0.03) and palm berries ($F_{5, 10}$ =4.23, P= 0.03) since they are seasonally available, but there was no significant difference among groups for acorn foraging ($F_{2, 10}$ =2.78, P= 0.11) or palm berry foraging ($F_{2, 10}$ =0.79, P= 0.48). Lemurs spent their greatest amount time consuming muscadine grapes from June through September averaging of 18 percent across groups (Figure 6). There was a significant difference in the proportion of time lemurs spent consuming grapevine throughout the year ($F_{5, 10}$ =9.22, P= 0.002). Laurel and Live oak leaves and stems were eaten year-round. However, the proportion of time lemurs spent foraging on oak leaves and stems also varied significantly throughout the year ($F_{5, 10}$ =6.13, P= 0.008; Figure 6).

Provisioning

The key management issue for St. Catherines Island is how free-ranging ringtailed lemurs use provisions. Although lemur groups spent similar amounts of *time* eating provisions, the *amount* they consumed varied among groups ($F_{2, 10}$ = 8.7, P= 0.006) and among bi-monthly time periods ($F_{5, 10}$ = 4.70, P= 0.018; Figure 7). Lemurs consistently consumed all of their provisioned fruit and vegetables. Amount of provisioned chow consumed varied from a low of about 31 grams of chow and 100 grams of fruit/vegetables per animal per day in the Oct/Nov bi-monthly time period to a high of 51 grams of chow and 100 grams of fruit/vegetables in the April/May bi-monthly time period. Overall, lemurs consumed an average of 39 grams of provisioned chow and 100 grams of fruit/vegetables per animal per day. Group A consumed more provisions than the other groups, showing the highest dependence on provisioned food for most months (Figure 7).

Home Range Assessment

I recorded a total of 395 GPS locations for Group A, 406 GPS locations for Group B, and 333 GPS locations for Group C. Annual home ranges for each group were projected onto a map of St. Catherines Island (Figure 1). Over the course of the entire study, Group A occupied a home range of 52.5 ha, Group B occupied a home range of 116.4 ha, and Group C occupied a home range of 42.4 ha (Figure 9). Groups had the greatest home range sizes in the spring and summer and the smallest range during the Oct/Nov period (Figure 9). There was a significant difference in home range size across groups ($F_{2,10}$ =6.9, P=0.01), with Group B having the largest home range size for most time periods throughout the year. There was no significant difference in home range size across months ($F_{5,10}$ =2.5, P=0.10; Figure 9). However, groups varied in which portion of their home range they used from month to month (Appendices A-C). The home range during any bi-monthly period was smaller (often much smaller) than the cumulative annual home range (Figure 9). The degree to which lemur space use shifted from month to month appeared to vary with season. During the winter months, lemur troops tended to use the same areas from month to month (consecutive bi-monthly home ranges showed high overlap; Figure 10). During other months, lemur troops tended to shift their home range from month to month (Figure 10).

Habitat Quality Assessment

Live oak, southern pines, and grapevine dominated the canopy in lemur habitats on SCI. Canopy cover differed among home ranges ($H= 21.6$, $df=2$, $P < 0.001$) with Groups A and B occupying relatively closed canopy forest (approximately 85% cover) and Group C occupying more open forest (Table 5). Percent ground cover did not differ significantly across groups (Table 5) but standard deviations were relatively large, suggesting that ground cover was patchy (Table 5).

Density and frequency of woody stems varied among home ranges (Table 6). Jaccard’s similarity index indicated that Group A had 38% of species in common with Group B and 35 % of species in common with Group C. Group B had 26% of species in common with Group C. There was no difference in the total number of stems in each groups’ habitat (Table 5). There was no difference in the number of forage species stems among groups (Table 5). In addition, there was no significant difference in the density ($H=1.10$, $df=2$, $P=0.58$) or frequency ($H=1.72$, $df= 2$, $P=0.42$) of forage species stems across the groups’ home ranges (Table 6).

The density and frequency of tree species were greatest for pine, oak, and cabbage palm trees. Red bay and wax myrtle trees were also important species in lemur habitats (Table 5). Tree basal area was approximately two times greater in Group A’s home range than Group C’s (Table 5). The large basal area of Group A and Group B’s habitats can be attributed to the presence of large oak and pine species. Although two thirds of Group C's basal area was pine and oak species, the remaining third was comprised of a variety of smaller tree species (Table 5). After excluding cabbage palm trees because diameter at breast height measurements were not reliable, there was no significant difference in the basal area of trees or the basal area of forage species trees across groups (Table 5).

Relationships among variables

Use if provisions might affect the time lemurs devote to foraging. All three lemur troops tended to forage less during bi-monthly periods when they consumed more provisions. However, only for Group C was this relationship significant Group C (r_s= -0.89, n=6, P= 0.02). I also expected home range size to be related to use of provisions and/or foraging. Larger home ranges were associated with less time spent foraging, but this relationship was not significant for any of group (Group A r_s= -0.54, n=6, P= 0.27; Group B r_s= -0.66, n=6, P=0.16; Group C r_s= -0.43, n=6, P=0.40). There was no significant relationship between home range size and time spent using provisions (Group A r_s= 0.54, n=6, P= 0.27; Group B r_s= 0.49, n=6, P= 0.33; Group C r_s= -0.09, n=6, P=87) or amount of provisions consumed for any group (Group A r_s= -0.09, n=6, P= 0.87; Group B r_s= 0.09, n=6, P= 0.87; Group C r_s= 0.26, n=6, P= 0.62). Although sample size was low for a meaningful test I also assessed the relationship between provisioning and home range size among groups (Table 7). There was no consistent relationship between home range size and overall provisioning use. Finally, I assessed the relationship between habitat characteristics and lemur activity. I compared vegetation measurements with amount of provisions, time spent foraging , and time spent consuming provisions. None of vegetation measurements were significantly correlated with any of these variables. In addition, there were no significant correlations between vegetation measurements and home range size.

To summarize, I found that there was no relationship between habitat quality and use of provisions or home range size (Table 7). The troop with the smallest home range size (Group C) did not use more of their provisions; the troop with the largest home range size (Group B) did consume the least amount of provisions. The troop with the greatest basal of forage species trees in their home range habitat (Group A) did not consume the least amount of provisions. The troop with the greatest number of forage stems in their home range habitat (Group C) also did not consume more of their provisions, but, however they did have the smallest home range size (Table 7).

CHAPTER 4

DISCUSSION

Understanding provisioning use in lemurs is important because provisioning has been identified as essential to successful reintroduction of primates, and it can facilitate the transition of captive animals to a free-ranging situation (Konstant and Mittermeier 1982, Tear and Ables 1999). However, pre-and post release supply of provisions can also be costly, and the degree to which animals depend on it varies in time and space. The costs of food and forage for zoos can be an important financial limitation. For example, the annual food and forage budget for the WSC for the primate collection is approximately $6000 for primate chow and $10,000 for fruit and vegetables. Dependence on provisioning may be reduced if the habitat that supports released individuals is sufficient enough to meet their dietary requirements. My study is the first detailed study of the use of provisions by the ringtailed lemurs on St. Catherines Island, a species which has been suggested to be a model for primate reintroduction (Keith-Lucas et al. 1999). There are four important conclusions from my study.

First, despite the fact that these lemur groups have been free-ranging on St. Catherines Island for several years (Table 1), they still use their provisions. The current balance between the use of natural foods and the use of provisions by lemurs on SCI has developed gradually. The first group of lemurs released on SCI was observed pulling branches of nearby red bay (*Persea borbonia*) into their cages and consuming the leaves. Keith-Lucas et al. (1999) found within six weeks post-release, 83% of the ringtailed lemurs' diet was comprised of provisioned food, and the remaining seventeen percent was forage items. Ten months after the troop was released, they only foraged on natural items in close proximity to the release site (Keith-Lucas et al. 1999). This suggests that it may take a substantial period of time for released captive-bred ringtailed lemurs to learn to forage, and that their dependence on provisioning is critical during the first several months post-release. In addition, although transitioned from captivity to a free-ranging situation on SCI, the lemurs used their provisions along with natural food.

Ganzhorn (1986) found that ringtailed lemurs living in a semi-free-ranging setting at the Duke University Primate Center spent a significantly greater proportion of their time consuming their chow and less time eating fruits and natural food items compared to brown lemurs (*Lemur fulvus*) who also lived in their multi-hectare enclosure. Compared to my results, the ringtailed lemurs in his study spent less of their activity budget eating (only about 12% vs. 20% in my study). His results suggested that food selection and foraging patterns of ringtailed lemurs reflect the behavior of an opportunistic frugivore that is adapted to a variable environment where food resources are turned over rapidly and the location of any food patch is not predictable (Ganzhorn 1986). Although lemurs on SCI spent more time consuming provisions than reported by Ganzhorn (1986), they still consumed only a portion of the provisions made available. In general, SCI lemurs consumed all of the fruit made available to them (100g/animal/day) but only about 35% of the chow available.

Second, the amount of provisions consumed by lemurs varies seasonally, and use of provisions does not appear to prevent response to variation in natural food supply. In general, my results are consistent with less use of provisions during periods of natural food abundance. Wild populations of ringtailed lemurs show variation in their foraging patterns that coincide with the availability and phenology of forage species (Sauther

1998). The lemurs in this study showed a similar pattern. My data show that there are sensitive periods when lemurs depend more on their provisions, such as winter and birthing season (Figure 11). Variation in use of natural foods also suggests lemurs are attentive to seasonal variation in natural food supply despite being provisioned. All three troops spent the greatest proportion of their time foraging and the least proportion of their time consuming provisions during the late summer/autumn. Because this is generally assumed to be a period of abundant natural food (such as fruits and seeds), it appears that the need to consume provisions was diminished by the presence of alternate natural forage. Phenological changes in plant resources may affect feeding preferences and feeding time in primates (Chapmin 1988). Dierenfeld and McCann (1999) found that the ringtailed lemurs in their study relied more heavily on seeds that were high in fat content during October and November and shifted to less nutrient dense foods in such as buds and leaves in early spring. The Live and Laurel oak (*Q. virginiana* and *Q. laurifolia*) trees that dominate the habitat on SCI are producing high fat, protein-rich acorns during the late summer/early autumn. Lemur spent the greatest proportion of time foraging on acorns and cabbage palm (*Sabal palmetto*) berries occurred during these months.

In the spring, however, lemurs were observed consuming more leaves (Figure 6). Dierenfeld and McCann (1999) described the fruits and leaves eaten by ringtailed lemurs on SCI as higher in fiber levels than those recommended for general primate dietary requirements. April and May were the months when the lemurs had the highest mean amount of provisions consumed per animal throughout the year (Figure 7), and they increased the amount time they spent foraging on laurel and live oak leaves (Figure 6). Buds eaten by ringtailed lemurs on SCI in the spring months had the highest level of protein of any food sampled (Dierenfeld and McCann 1999). Females are beginning to lactate after a period of low seasonal productivity in terms of leaves, fruits, and seeds. In Madagascar there are two peaks of fruit availability, one during the birth/lactation period (October-November for wild populations) and one during the late-lactation/weaning period (March-April for wild populations) for ringtailed lemurs (Sauther 1998). Due to hemispheric differences, these periods are reversed on SCI. Wild ringtailed lemurs tend to seek out resources that maximize leaf water content and protein during the birthing season (Mertl-Millhollen et al. 2003). The ringtailed lemurs on SCI were observed eating grapevine leaves and buds, Laurel Cherry leaves and berries, Red bay leaves and berries, and sparkleberry leaves and buds during this time period (Figure 6). The foraging behavior of the ringtailed lemurs in my study suggests that lemurs may be relying more on their provisioned food and protein-rich forage items during the birthing season. This is consistent with wild populations.

Third, the observed shift in space use by lemurs also suggests that they respond to seasonal shifts in natural food. Home ranges were centered on each troop’s shelter site. However the size and geographical location of home ranges varied through the year. Some of this variation was consistent with lemur responses to seasonal variation in habitat. Most notably, troop home range sizes were smallest during the October/November bi-monthly time period (Figure 9) when they ate the least amount of their provisions. This was probably due to the distribution and abundance of Laurel and live oak trees producing acorns in the home range, offsetting the need to consume provisions for lemurs. Laurel and live oaks were common in all the troops’ home ranges (Table 6). Therefore, lemur troops would not have to range far during this time period to have access to a densely distributed food resource. Home ranges were largest during the Feb/March and Jun/July bi-monthly time period. Groups foraged more on the buds and new leaves of trees during these months. This may explain why troops traveled longer distances and ranged more during these months. They may have decreased ranging during April and May because of birthing season when they may have relied more on the reliability of their provisions during this physiologically stressful time. In conclusion, all three troops stayed in a core range from October through January and varied in their travel patterns and home range use more from February though August (Figure 10). Studies on home range sizes of ringtailed lemurs do not detail seasonal home range changes but rather compare home range sizes of individual troops to one another or from year to year (Budnitz and Dainis 1975; Budnitz 1978; Sussman 1991; However, Sauther (1998) and Mertl-Millhollen et al. (2003) have shown that lemurs respond to seasonal changes in their environment in terms of forage and natural food use. Home range size and natural food use in the lemurs on St. Catherines Island do appear to be related, however, no significant correlations were found in my analysis on these variables. This may be due to the fact that the three troops occupy similar habitats.

On SCI lemur troops avoided one another as they do in the wild (Jolly 1972), but contradictory to some wild populations of ringtailed lemurs, each group appeared to have exclusive use of its home range habitat (Sussman 1991) except for the few regions on the boundaries of each groups' home range where troops encounters typically took place (Figure 1). Lemurs primarily traveled through their home ranges by using pre-exiting roads and secondarily by crossing in the treetops. At times, troops were observed traveling in the mid-story of the forest while foraging.

Finally, there was no strong tie between provisioning use and home range size or habitat quality. Use of provisions was not ultimately correlated with home range size or specific features of the habitat (Table 7). Thus, there is a looser relationship between habitat and home range for the ringtailed lemurs on SCI than has been observed with wild populations (Budnitz and Dainis 1975; Budnitz 1978; Sussman 1991). Despite changes in amount of provisions consumed and home range size, there was no evident relationship between these two variables. Amount of provisions used and home range size both varied seasonally, yet there was no significant difference in home range size across the year for lemur troops. Thus, habitat and foraging, not provisioning use, seems to drive home range size. Home ranges abundant with food resources are smaller for ringtailed lemurs in the wild (Budnitz and Dainis 1975; Budnitz 1978; Sussman 1991). Annual home range size was smallest for Group C. This would suggest that Group C had a habitat that was rich in terms of forage items and that forage species were densely distributed. Group C had the highest density of all forage species stems (Table 6). However, Group C had lower basal area of forage species trees than the other groups.

In summary this study was to document baseline seasonal dependence on provisioned diets and home range size of the ringtailed lemur troops on SCI. I determined that during the fall months, ringtailed lemur troops on SCI ranged less and consumed less of their provisions. I also determined that during the birthing and lactation periods, ringtailed lemurs tended to rely more heavily on their provisions, even with the amount of supplemental food increased to meet the dietary requirements of these animals (Figure 11). Although, I was not able to show how habitat differed seasonally, I concluded that the ringtailed lemurs differed in their home range habitat in terms of abundance and composition of tree and plant species. Although lemurs used their provisions differentially through time, their choice of forage items and use of habitat changed throughout the year. Finally, it appears that provisioning ringtailed lemurs on SCI does not appear to deter natural foraging or ranging behaviors across seasons.

Management Implications

My study has three important management implications. First, these data from my study suggest that WSC could reduce the amount of provisioned chow by almost half without altering observed patterns of consumption. Managers use the provisions to ensure monitoring of the animals on a daily basis. However, this study shows that it would be cost-effective to reduce provisioned chow. This study provides the baseline assessment of seasonal dependence on provisioned diets and shows that lemurs do not consume more that half of the provisioned chow offered to them on a daily basis, yet they consistently consume the total amount of their fruit and vegetables. Based on the data provided in this study, provisioned chow to 57g/animal/day particularly during the fall when natural foods are abundant.

Second, provisioning does not inhibit lemur responses to natural variation in food. Therefore, provisioning lemurs on SCI allows for routine monitoring of the animals, but it does not prevent the animals from engaging in natural behaviors that would be necessary for survival if the potential for reintroduction or translocation becomes a reality. Decreasing the amount of provisioned chow, which is nutritionally complete may allow for future research on nutrient intake from natural food by lemurs on St. Catherines Island. Dierenfeld and McCann (1999) showed that annual weighted means of forage selected by lemurs were low in protein and high in fiber relative to estimates of dietary requirements for non-human primates. Their study shows that lemurs are foraging on items that meet their nutritional needs.

Third, this study could be generalizable to other diurnal lemurs (except for dietary specialists). This study shows provisioning may prove to be a necessary conservation tool in the transition of captive lemurs animals to a release situation, but possibly, unnecessary once the troops have acclimated to their new habitat. Given that their native habitat has decreased by almost 65 percent, provisioning may be an essential management technique for wild populations (Sussman et al. 2003). However, it is important to realize that the resources lost through deforestation are not only critical forage species for lemurs, lemurs are experiencing a complete alteration of their habitat in the wild. Given that lemurs are sensitive to seasonal changes in the phenology of their habitat (Mertl-Millhollen et al. 2003) and that they tend to cluster in regions of closed canopy (Budnitz and Dainis, 1975), they will be faced with new challenges in their disturbed forests. Ringtailed lemurs have been described as opportunistic and able to adapt to changes in their environment (Ganzhorn 1986). Their adaptability as a species may prove to ensure their survival given the environmental changes in their native habitat. The SCI ringtailed lemurs serve as model system for reintroduction and future research on the effects of provisioning may elucidate a cleared picture of their dependence on provisions and the ecological constraints on home range size and habitat use. Experiments are needed to determine if the ringtailed lemur could survive on minimal or no provisioned food. Given there are several troops of lemurs on SCI, an experimental design could be employed to examine troops' responses to different conditions of available provisioning. It may be the case that lemurs respond by increasing their home range size. In addition, a more precise evaluation of the habitat and of seasonal productivity of the plants and trees is needed. A more rigorous evaluation of available forage may show a closer relationship between home range size and habitat quality as evidenced in the wild (Budnitz and Dainis 1975; Budnitz 1978; Sussman 1991). Subsequent studies such as these on the ringtailed lemurs would provide critical information that will be important in determining the location and spatial requirements of reintroduced or translocated troops of lemurs and the role of provisioning.

Table 1. Troop composition of released ringtailed lemurs on St. Catherines Island, 1985- 2003. (M= males, F= Females, J= juveniles and infants).

Year Formed	Lemur Group	Original Composition			Composition July 2002			Composition July 2003		
		Males	Females	Juveniles	Males	Females	Juveniles	Males	Females	Juveniles
1985	Troop 1	2	4	0	6	6	5	N/A	N/A	N/A
1986	Group A[1]	1	1	4	4	8	6	5	8	6
1994	Group B[1]	2	2	0	4	9	6	2	8	9
2000	Group C[1]	1	4	0	4	4	6	2	4	7

[1] troops used in this study

Table 2. Ethogram of ringtailed lemur behaviors recorded during this study on St. Catherines Island, 2002-2003. Ethogram is based on Parga (2002).

Behavior	Description
Provision	Animal actively consumed provisioned food consisting of chow, fruits, and vegetables. Provisioning began with an animal handling and eating the provisioned items.
Locomote ground	Animal walked and moved on the ground substrate. This behavior was distinguished from “Travel”. This terrestrial behavior usually involves walking on all four limbs, however, ringtailed lemurs can also locomote on their two hind legs.
Locomote vertical	Animal actively climbed or moved about above the ground on either a man-made or natural substrate. This behavior usually involved climbing trees, leaping from tree to tree, jumping in trees, and general moving in trees.
Travel	Animal or the troop moved in a directed manner to a new location. This could occur either in the treetops, or, most usually, on the ground. Traveling usually involved coordinated troop movement, often on the existing dirt roads. Traveling involved fast locomotion that was usually organized and had direction as opposed to relocating or moving about in trees or on the ground.
Scent Mark	Animal marked a tree or man-made object with either its ano-genital region (for females) and/or brachial spurs (for males).
Rest Ground	Animal sat or stopped on the ground. This position usually involved sitting on rear haunches alone or with others in the troop. Grooming often occurred in the rest position. This is distinguished from “Sun Ground” and “Sleep”.
Rest Vertical	Animal rested in a tree or on a man-made structure above the ground. This behavior usually involved grooming with other animals but also occurred when animals were alone. This is distinguished from “Sun Vertical” and “Sleep”.
Sleep	Animal actively sleeping or falling asleep, often huddled with a group of other animals. Sleep can be interrupted by the movement of other animals momentarily, but once a sleep session has started, this behavior was continuously recorded until an animal began stretch and sit up from the sleeping position for more than one minute.

Table 2. (continued)

Behavior	Description
Forage	Animal actively eating natural vegetation. Foraging began when an animal started to eat part of a plant and continued as the animal sought and consumed plant parts. When foraging occurred, the species and part of the plant were also recorded.
Drink	Animal actively drinking water from provisioned water bottle, ground, tree-trunk or other natural reservoir.
Sun Ground	Animal actively sunning itself on the ground. "Sunning" behavior occurs when an animal faces its ventral side toward the sun with its arms outstretched, balancing on its legs and buttocks to warm itself in colder temperatures.
Sun Vertical	Animal actively sunning itself in trees or on a man-made structure.

Table 3. Plants and trees observed being eaten by ringtailed lemur troops during this study on St. Catherines Island, GA. List does not include unknown grasses that were occasionally consumed by lemurs.

Species	**Common Name**	**Plant part**
Acer rubrum	Red Maple	Leaves
		Buds
Ilex opaca	American Holly	Leaves
		Berries
Magnolia grandiflora	Southern Magnolia	Leaves
		Buds, flower buds
Melia azedarach	Chinaberry	Berries
Myrica cerifera	Wax myrtle	Leaves
		Berries
Persea borbonia	Red bay	Leaves
		Berries
Pinus elliottii	Slash Pine	Shoots, stalks
		Seeds
Pinus palustris	Longleaf pine	Shoots, stalks
		Seeds
Pinus taeda	Loblolly Pine	Shoots, stalks
		Seeds
Polypodium polyploides	Resurrection fern	Leaves
Prunus caroliniana	Carolina laurel cherry	Leaves
		Fruit, berries
Pterocaulon pycnostachyum	Black-root	Leaves
		Buds
		Flowers
Quercus laurifolia	Laurel oak	Leaves
		Buds
		Acorns
Quercus nigra	Water Oak	Leaves
		Buds
Quercus virginiana	Live oak	Leaves
		Buds
		Acorns
Sassafras albidum	Sassafras	Leaves
Sabal palmetto	Cabbage Palm	Fruit
		Berries
		Stalk, bark
Serenoa repens	Saw Palmetto	Stalk, bark
Smilax laurifolia	Bamboo vine	Leaves
		Vine
Tillandsia usneoides	Spanish Moss	Leaves
Toxicodendron radicans	Poison Ivy	Leaves
Vaccinium arboreum	Sparkleberry	Leaves
		Flower Buds
		Berries
Vitis rotundifolia	Muscadine grape	Leaves
		Buds
		Fruit
		Vine
Zanothoxylum clava-herculis	Hercules' Club	Leaves

Table 4. Mean (+SE) proportion of time engaged in behavior per scan for each bi-monthly time period and for total sampling period for ringtailed lemur troops on St. Catherines Island, 2002-2003. Behaviors are listed in order of decreasing total frequency.

Behavior	**Group**	**Jun/July**	**Aug/Sept**	**Oct/Nov**	**Dec/Jan**	**Feb/Mar**	**Apr/May**	**Total**
Rest Vertical	A	0.380 (0.03)	0.263 (0.04)	0.196 (0.05)	0.353 (0.06)	0.255 (0.03)	0.244 (0.03)	0.296 (0.02)
	B	0.380 (0.04)	0.185 (0.04)	0.136 (0.03)	0.182 (0.05)	0.248 (0.04)	0.297 (0.03)	0.258 (0.02)
	C	0.395 (0.04)	0.280 (0.04)	0.224 (0.04)	0.305 (0.05)	0.261 (0.04)	0.321 (0.03)	0.305 (0.02)
Sleep	A	0.115 (0.03)	0.108 (0.05)	0.116 (0.05)	0.268 (0.08)	0.274 (0.05)	0.111 (0.03)	0.165 (0.02)
	B	0.090 (0.03)	0.218 (0.07)	0.285 (0.08)	0.103 (0.05)	0.263 (0.05)	0.230 (0.04)	0.199 (0.02)
	C	0.218 (0.12)	0.109 (0.04)	0.150 (0.06)	0.172 (0.07)	0.295 (0.06)	0.258 (0.05)	0.213 (0.02)
Locomote Vertical	A	0.169 (0.02)	0.185 (0.03)	0.212 (0.00)	0.107 (0.02)	0.110 (0.02)	0.110 (0.02)	0.143 (0.01)
	B	0.115 (0.02)	0.216 (0.04)	0.115 (0.03)	0.123 (0.02)	0.098 (0.02)	0.102 (0.02)	0.122 (0.01)
	C	0.090 (0.02)	0.203 (0.03)	0.146 (0.02)	0.126 (0.02)	0.104 (0.02)	0.073 (0.01)	0.113 (0.01)
Forage	A	0.110 (0.02)	0.181 (0.04)	0.150 (0.05)	0.056 (0.02)	0.132 (0.03)	0.083 (0.03)	0.115 (0.01)
	B	0.072 (0.02)	0.141 (0.04)	0.110 (0.03)	0.106 (0.03)	0.073 (0.03)	0.090 (0.02)	0.094 (0.01)
	C	0.098 (0.03)	0.154 (0.04)	0.321 (0.06)	0.143 (0.05)	0.113 (0.03)	0.086 (0.02)	0.136 (0.01)
Provision	A	0.097 (0.02)	0.054 (0.02)	0.057 (0.02)	0.138 (0.05)	0.060 (0.02)	0.116 (0.03)	0.090 (0.01)
	B	0.096 (0.02)	0.084 (0.03)	0.072 (0.02)	0.113 (0.03)	0.125 (0.03)	0.087 (0.02)	0.096 (0.01)
	C	0.053 (0.02)	0.102 (0.03)	0.043 (0.01)	0.105 (0.04)	0.072 (0.02)	0.109 (0.03)	0.082 (0.01)
Rest Ground	A	0.040 (0.01)	0.060 (0.03)	0.055 (0.02)	0.016 (0.01)	0.076 (0.03)	0.107 (0.03)	0.061 (0.01)
	B	0.065 (0.02)	0.028 (0.00)	0.103 (0.04)	0.146 (0.04)	0.068 (0.02)	0.094 (0.02)	0.081 (0.01)
	C	0.034 (0.01)	0.025 (0.01)	0.012 (0.01)	0.048 (0.02)	0.061 (0.01)	0.074 (0.02)	0.047 (0.01)
Locomote Ground	A	0.035 (0.00)	0.037 (0.01)	0.089 (0.04)	0.033 (0.01)	0.026 (0.00)	0.058 (0.01)	0.042 (0.01)
	B	0.060 (0.01)	0.055 (0.02)	0.083 (0.02)	0.093 (0.02)	0.057 (0.01)	0.050 (0.01)	0.063 (0.01)
	C	0.036 (0.01)	0.042 (0.01)	0.060 (0.01)	0.051 (0.02)	0.038 (0.01)	0.038 (0.01)	0.044 (0.01)

Table 4. (continued)

Behavior	Group	Jun/July	Aug/Sept	Oct/Nov	Dec/Jan	Feb/Mar	Apr/May	Total
Travel	A	0.029 (0.01)	0.052 (0.02)	0.036 (0.03)	0.000 (0.00)	0.022 (0.01)	0.058 (0.03)	0.033 (0.01)
	B	0.090 (0.03)	0.051 (0.02)	0.036 (0.02)	0.028 (0.01)	0.032 (0.02)	0.031 (0.01)	0.046 (0.01)
	C	0.056 (0.02)	0.051 (0.02)	0.000 (0.00)	0.007 (0.01)	0.032 (0.01)	0.008 (0.01)	0.028 (0.01)
Sun Vertical	A	0.000 (0.00)	0.050 (0.04)	0.055 (0.04)	0.022 (0.01)	0.028 (0.01)	0.066 (0.02)	0.037 (0.01)
	B	0.000 (0.00)	0.000 (0.00)	0.039 (0.03)	0.072 (0.05)	0.015 (0.01)	0.000 (0.00)	0.015 (0.01)
	C	0.003 (0.02)	0.000 (0.00)	0.038 (0.03)	0.029 (0.02)	0.016 (0.01)	0.010 (0.09)	0.014 (0.00)
Scent Mark	A	0.007 (0.00)	0.006 (0.00)	0.002 (0.01)	0.005 (0.00)	0.005 (0.00)	0.011 (0.00)	0.008 (0.00)
	B	0.020 (0.01)	0.015 (0.01)	0.015 (0.00)	0.007 (0.00)	0.005 (0.00)	0.016 (0.00)	0.013 (0.03)
	C	0.013 (0.00)	0.014 (0.00)	0.013 (0.00)	0.005 (0.00)	0.003 (0.00)	0.013 (0.00)	0.011 (0.02)
Drink	A	0.013 (0.00)	0.000 (0.00)	0.002 (0.00)	0.001 (0.00)	0.005 (0.00)	0.008 (0.00)	0.006 (0.00)
	B	0.007 (0.00)	0.000 (0.00)	0.000 (0.00)	0.001 (0.00)	0.011 (0.01)	0.003 (0.00)	0.004 (0.00)
	C	0.003 (0.00)	0.007 (0.00)	0.000 (0.00)	0.000 (0.00)	0.000 (0.00)	0.004 (0.00)	0.003 (0.00)
Sun Ground	A	0.000 (0.00)	0.002 (0.00)	0.009 (0.01)	0.000 (0.00)	0.006 (0.01)	0.008 (0.00)	0.004 (0.00)
	B	0.003 (0.00)	0.000 (0.00)	0.007 (0.01)	0.010 (0.01)	0.013 (0.01)	0.001 (0.01)	0.005 (0.00)
	C	0.000 (0.00)	0.001 (0.01)	0.007 (0.01)	0.000 (0.00)	0.006 (0.00)	0.002 (0.00)	0.002 (0.00)

Table 5. Vegetation measurements of ringtailed lemur troop home range habitats on St. Catherines Island, 2002-2003. Stem count included all woody stems (<3m). Basal area included all trees (>3m). Total list of species and part of plant consumed by ringtailed lemurs is given in Table 3.

Measurement	**Group A**		**Group B**		**Group C**		**Significance**		
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**H**	**df**	**P value**
Canopy Cover (%)	88.58	2.16	82.19	4.19	64.22	5.47	21.6	2	<0.001
Ground cover per m^2 (%)	28.04	30.95	22.16	31.07	30.97	37.87	0.06	2	0.97
Stem count (stem/ m^2)	0.46	0.10	0.69	0.16	2.50	0.72	2.40	2	0.30
Stem count of forage species (stem/m^2)	0.10	0.03	0.27	0.08	0.54	0.23	2.50	2	0.29
Basal area (m^2/ha)	31.43	6.46	27.08	5.33	17.58	3.47	1.91	2	0.39
Basal area (m^2/ha) of forage species	30.87	6.35	24.35	4.79	15.11	3.21	1.66	2	0.44
Total Basal Area of forage species (m^2/ha)									
Magnolia grandiflora	2.28		0		0.88				
Myrica cerifera	0		0.0002		1.14				
Quercus laurifolia and q. virginiana	13.49		8.83		5.87				
Quercus nigra	0		0		0.30				
Persea borbonia	0.22		0.63		1.44				
Pinus Species	14.79		14.89		4.94				
Prunus caroliniana	0.087		0		0				
Vaccinium arboreum	0		0		0.54				

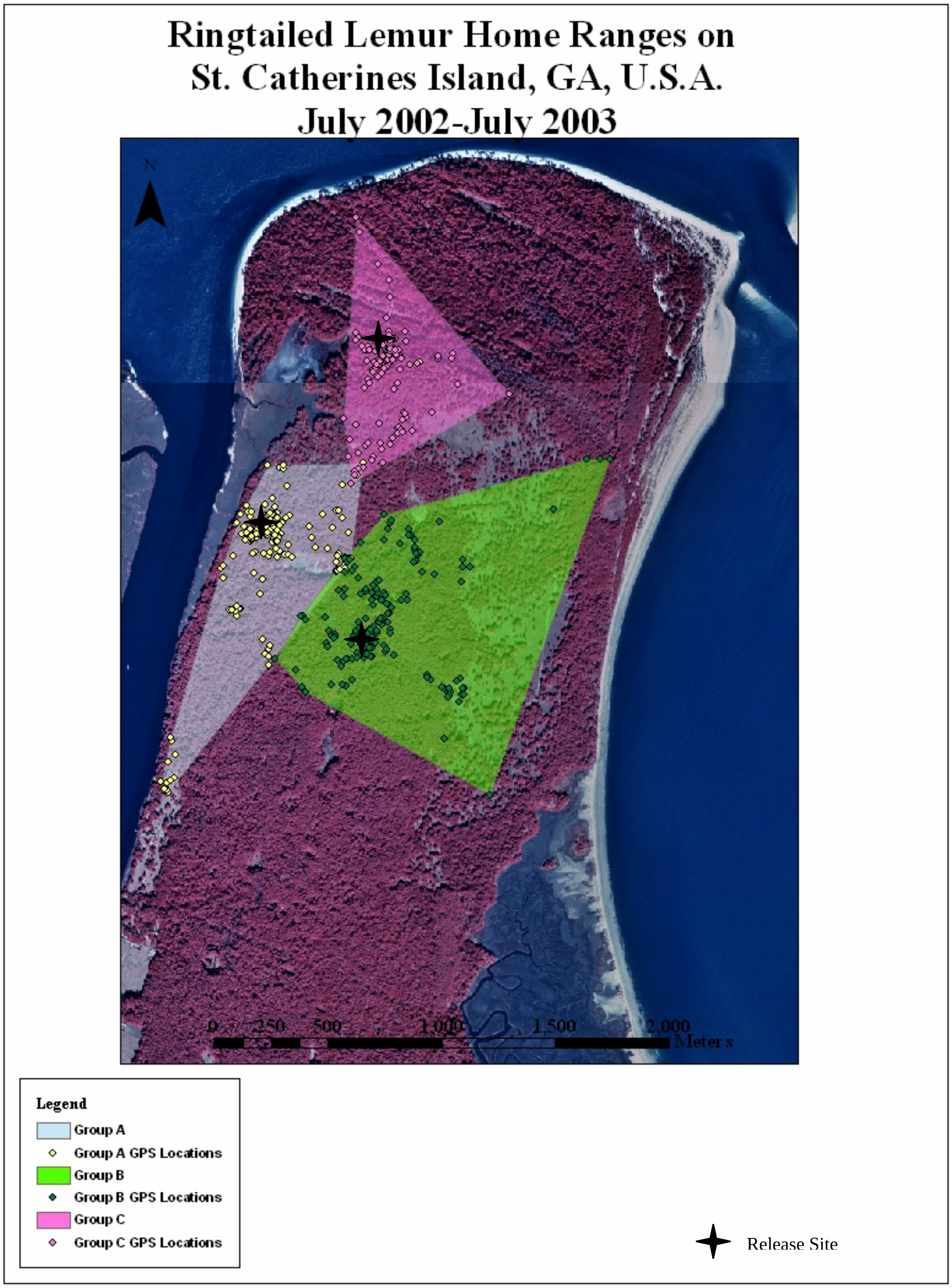
Table 6. Density (stems or trees/m^2) and frequency (proportion of plots occupied by species) of plants and trees ringtailed lemurs were observed consuming on St. Catherines Island, 2002-2003.

Group A			**Group B**			**Group C**		
Species	**Density**	**Frequency**	**Species**	**Density**	**Frequency**	**Species**	**Density**	**Frequency**
Stems								
Myrica cerifera	0	0	*Myrica cerifera*	0.09	0.17	*Myrica cerifera*	0.12	0.08
Pinus species	0.03	0.10	*Pinus species*	0.06	0.24	*Pinus species*	0.11	0.04
Pterocaulon pycnostachyum	0	0	*Pterocaulon pycnostachyum*	0.07	0.13	*Pterocaulon pycnostachyum*	0.27	0.10
Sabal palmetto	0.04	0.32	*Sabal palmetto*	0.01	0.07	*Sabal palmetto*	0.03	0.01
Serenoa repens	0.04	0.03	*Serenoa repens*	0.03	0.04	*Serenoa repens*	0.04	0.03
Trees								
Magnolia grandiflora	0.002	0.08	*Magnolia grandiflora*	0	0	*Magnolia grandiflora*	0.0003	0.03
Myrica cerifera	0	0	*Myrica cerifera*	0.011	0.04	*Myrica cerifera*	0.007	0.17
Persea borbonia	0.001	0.04	*Persea borbonia*	0.003	0.15	*Persea borbonia*	0.004	0.13
Pinus Species	0.019	0.40	*Pinus Species*	0.018	0.48	*Pinus Species*	0.013	0.41
Prunus caroliniana	0.003	0.03	*Prunus caroliniana*	0	0	*Prunus caroliniana*	0	0
Quercus Species	0.005	0.36	*Quercus Species*	0.004	0.22	*Quercus Species*	0.003	0.27
Quercus nigra	0	0	*Quercus nigra*	0	0	*Quercus nigra*	0.0003	0.03
Sabal palmetto	0.009	0.23	*Sabal palmetto*	0.006	0.07	*Sabal palmetto*	0.002	0.20
Serenoa repens	0.0003	0.03	*Serenoa repens*	0.001	0.04	*Serenoa repens*	0.0003	0.03
Vaccinium arboreum	0	0	*Vaccinium arboreum*	0	0	*Vaccinium arboreum*	0.003	0.13

Table 7. Summary of home range size, provisioning use, and habitat measurements for ringtailed lemur groups on St. Catherines Island, 2002-2003.

	Group		
	A	**B**	**C**
Total home range size (m^2/ha)	52.58	116.4	42.43
Mean home range size (m^2/ha)	26.50	45.97	11.98
Mean provision use (gm)	146.78	132.61	138.05
Basal area of forage species (m^2/ha)	30.87	24.35	15.11
Stem count of forage stems (stem/m^2)	0.10	0.27	0.54

Figure 1. Map of St. Catherines Island reflecting overall lemur ranges throughout this study.



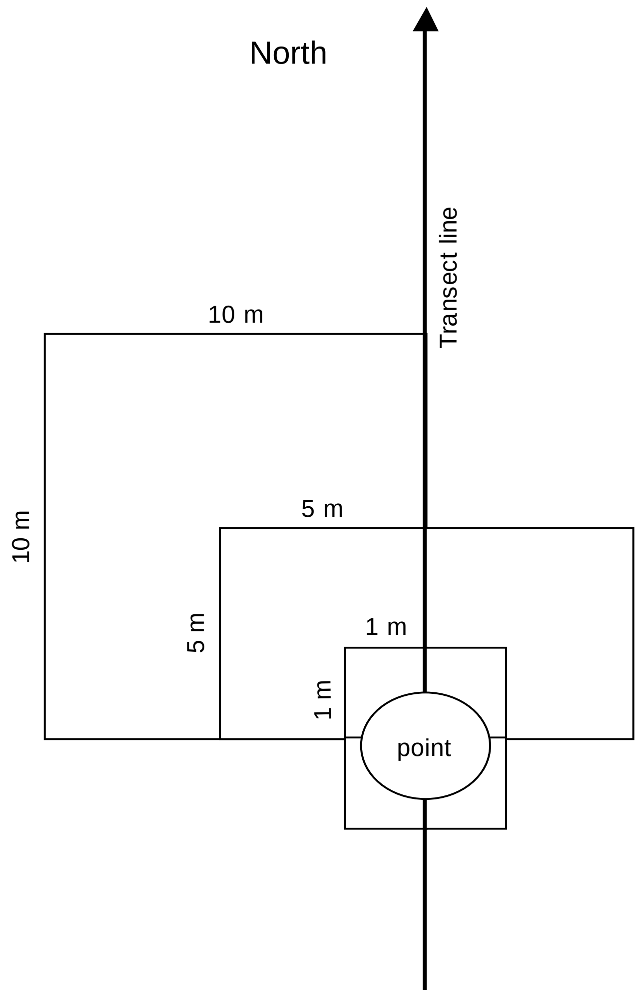


Figure 2. Sampling design for quantifying vegetation. Canopy cover was estimated by reading a densiometer at each cardinal compass point while standing directly on the point. Percent ground cover was estimated in four 1x1-m grids centered on the sampling point. Woody stem density and species count were measured in two 5x5-m grids adjacent to the transect line. Basal area and tree species count were measured in one 10x10-m grid adjacent to the transect line.

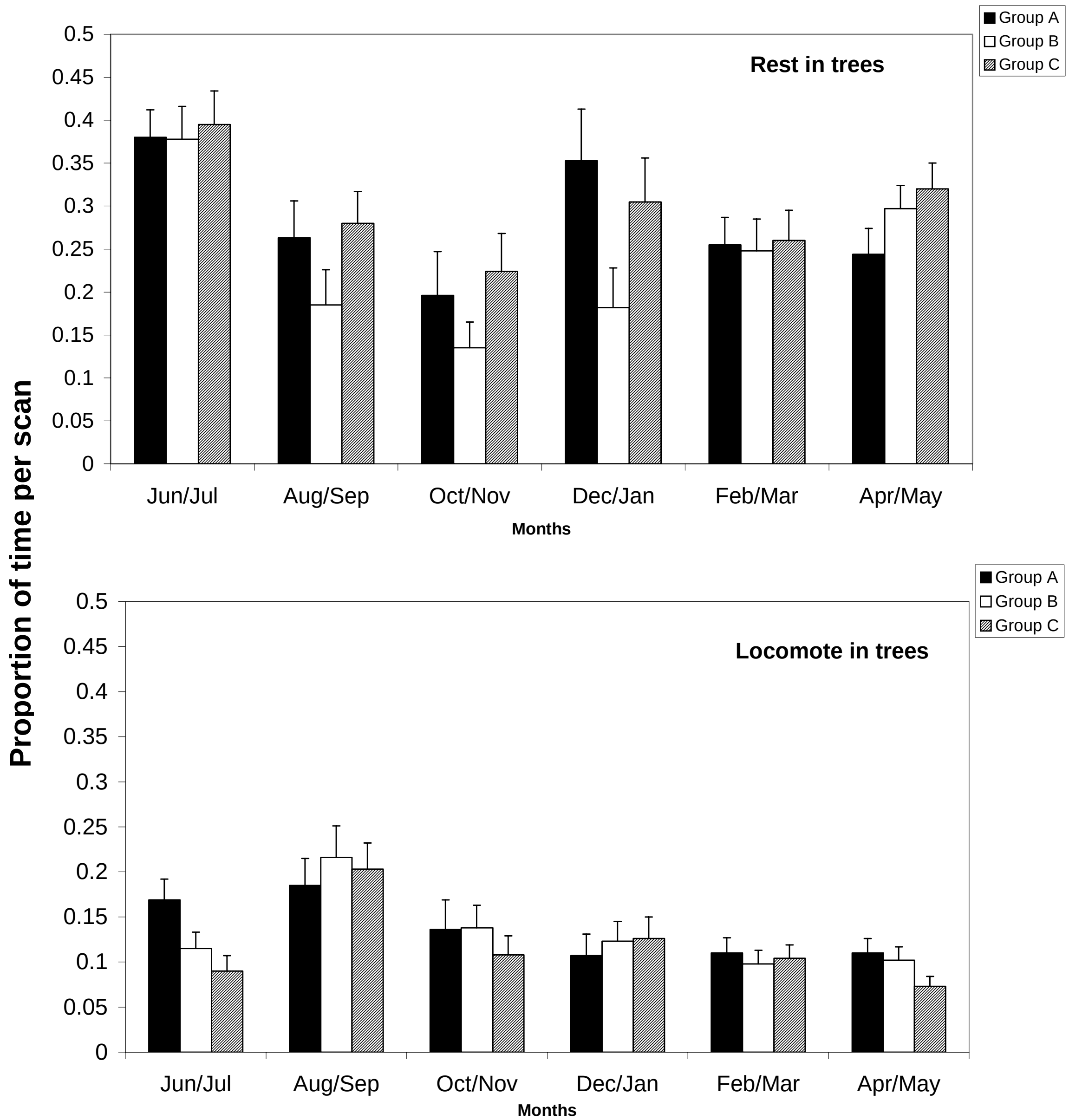


Figure 3. Proportion of time (mean +SE) spent resting in trees and locomoting in trees during each time period for ringtailed lemur troops on St. Catherines Island, 2002-2003.

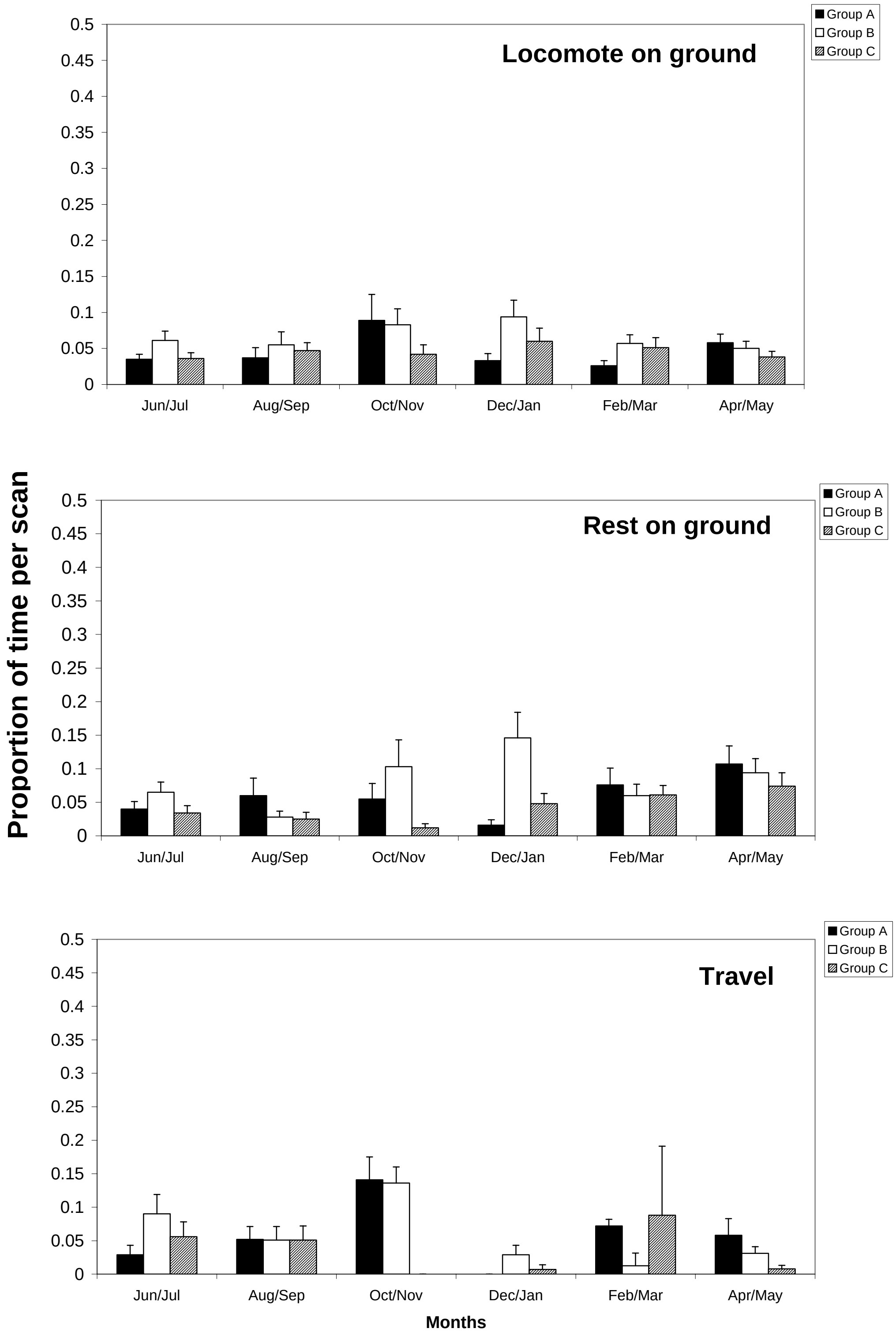


Figure 4. Proportion of time (mean +SE) spent locomoting on the ground, resting on the ground, and traveling during each time period for ringtailed lemur troops on St. Catherines Island, 2002-2003.

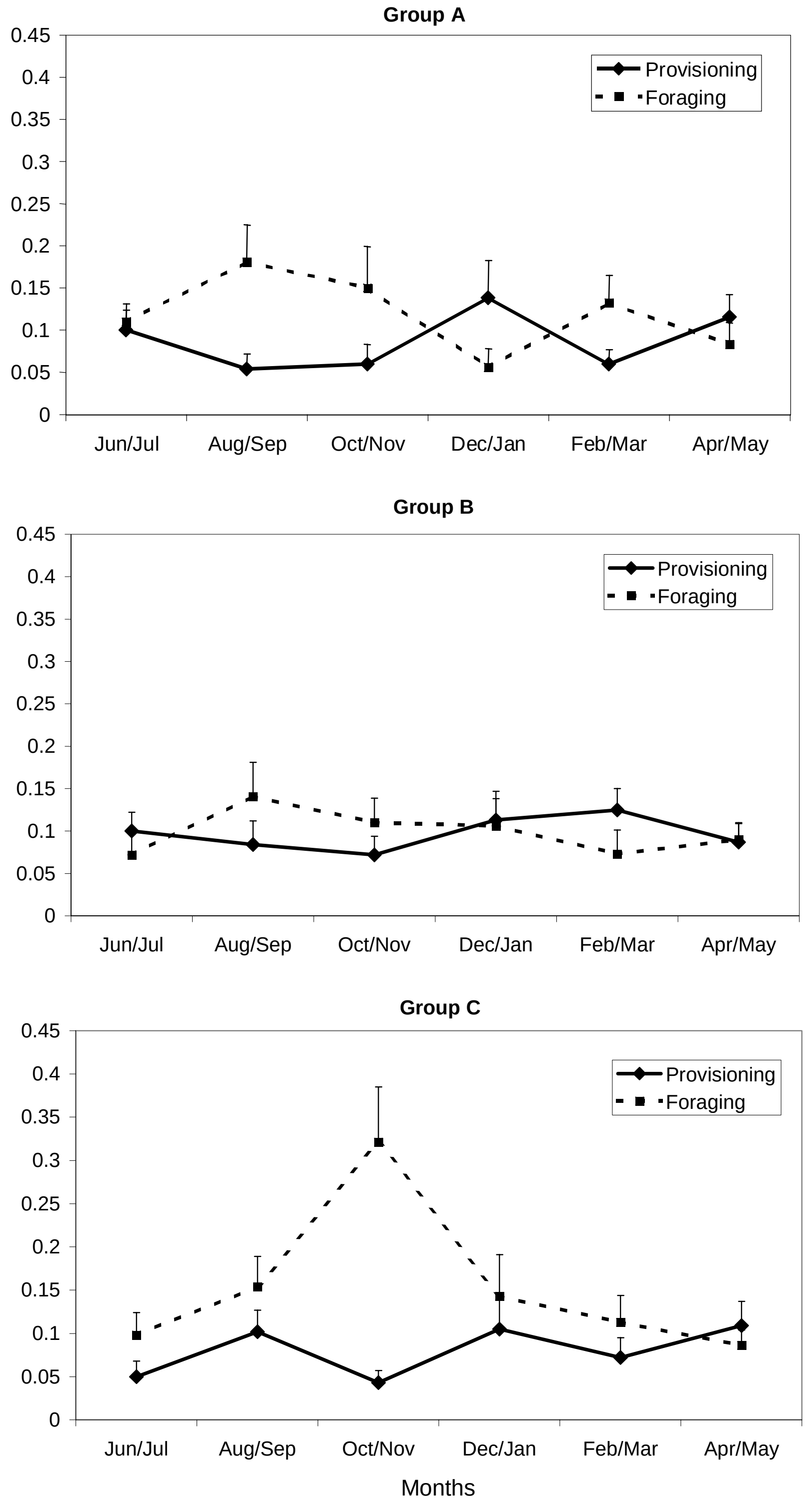


Figure 5. Proportion of time (mean +SE) spent consuming provisions and foraging during each time period for ringtailed lemur troops on St. Catherines Island, 2002-2003.

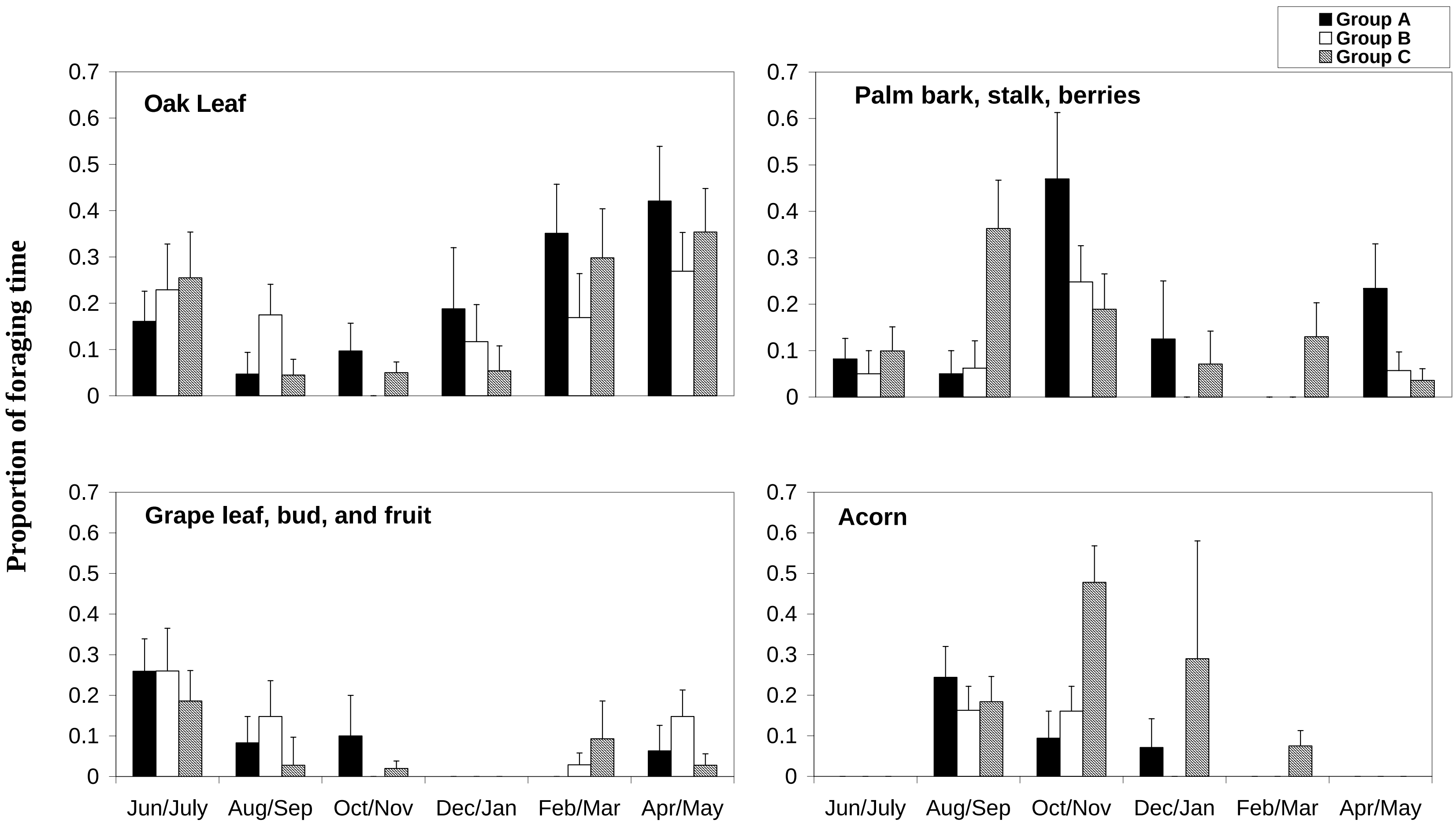


Figure 6. Proportion of time spent (mean +SE) foraging on natural items for ringtailed lemur troops on St. Catherines Island, 2002-2003.

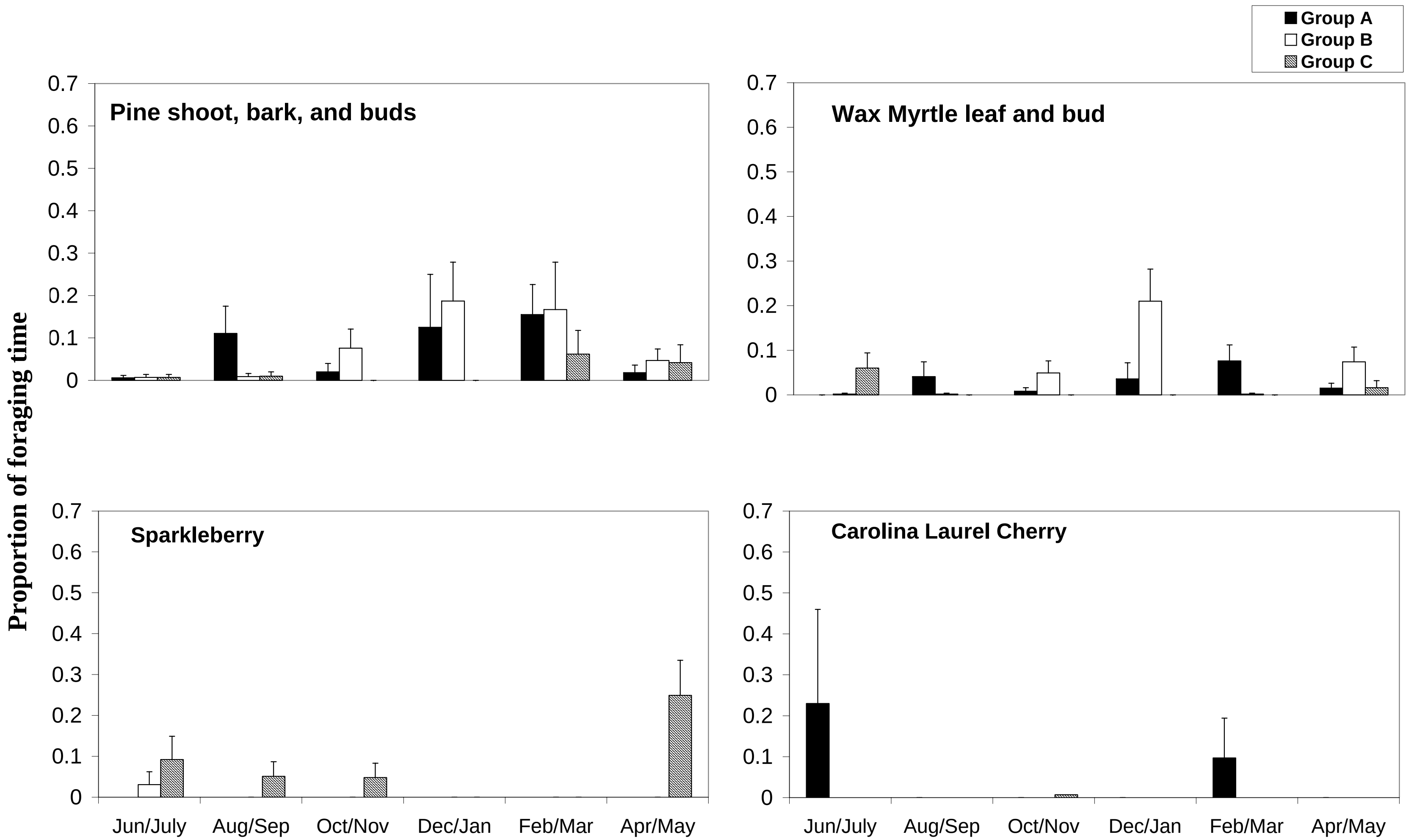


Figure 6. (continued)

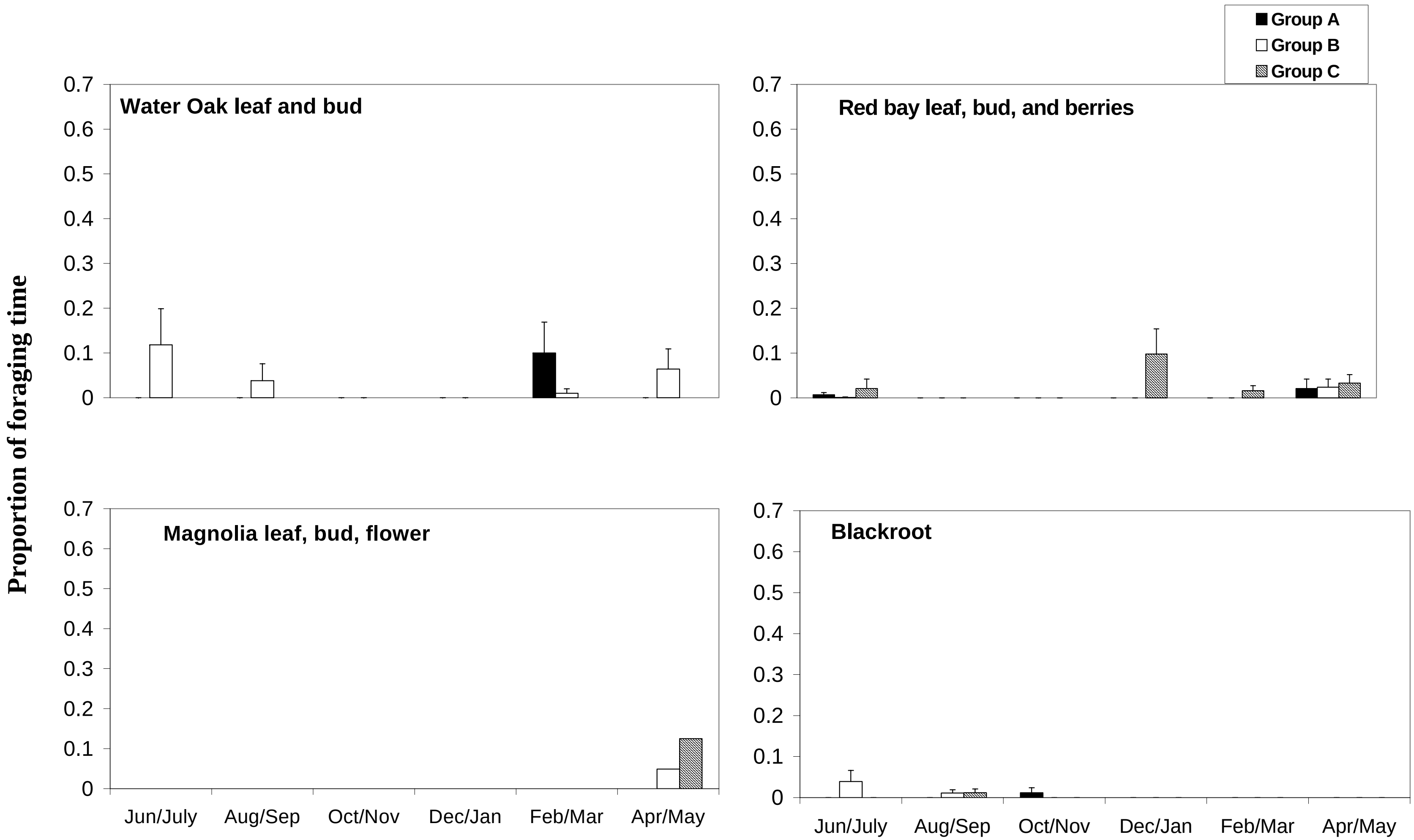


Figure 6. (continued)

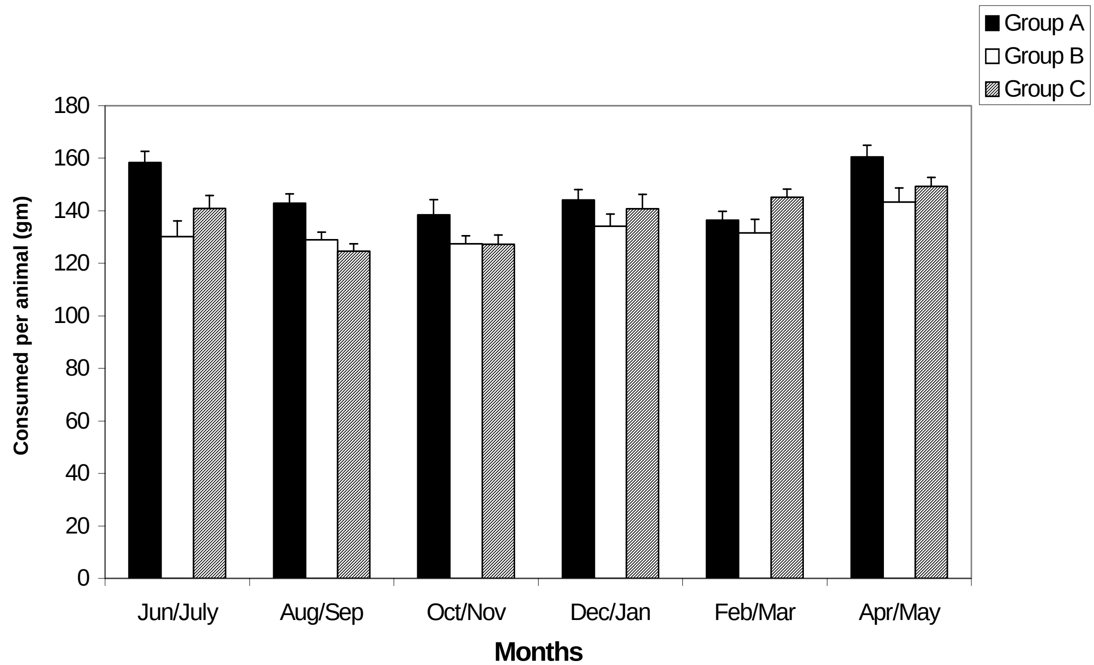


Figure 7. Amount of provisioned food (mean +SE) consumed per animal during each time period for ringtailed lemur troops on St. Catherines Island, 2002-2003.

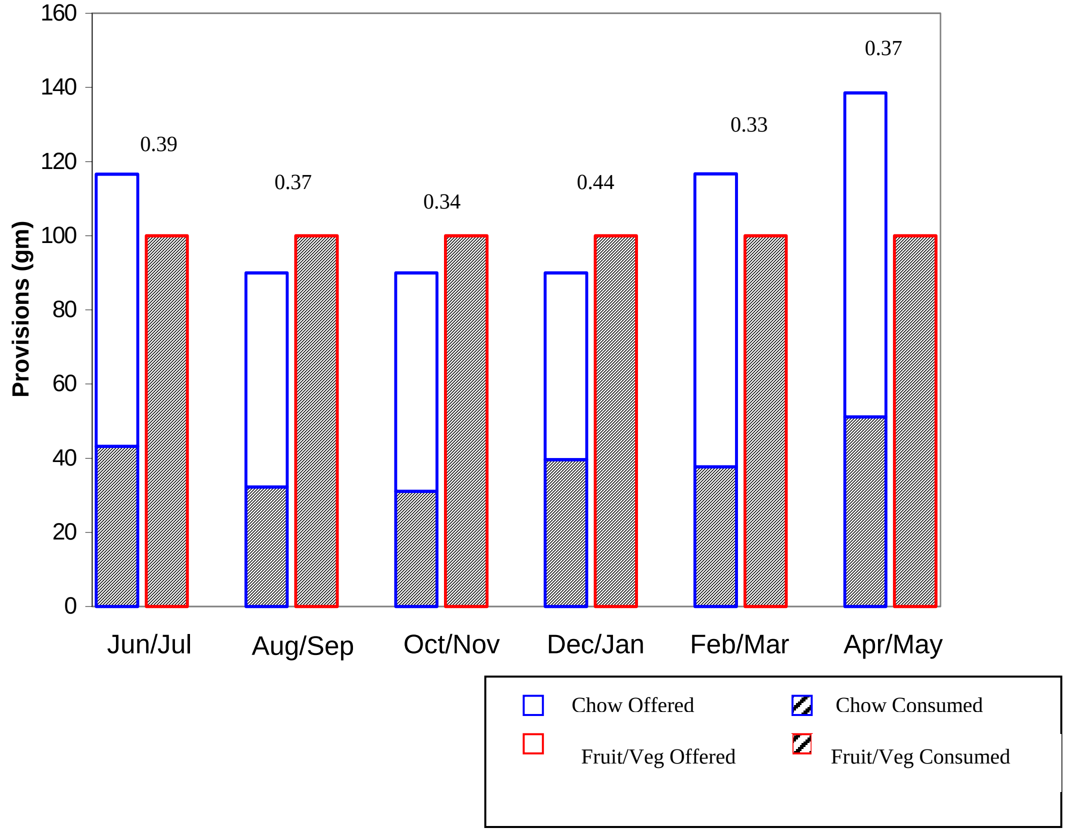
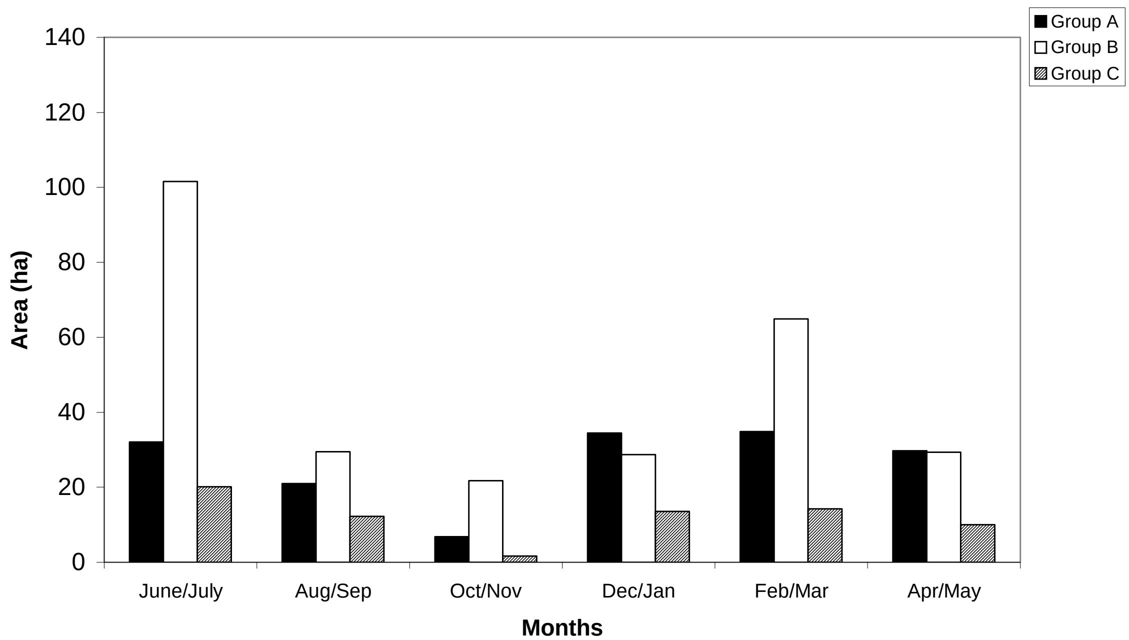


Figure 8. Mean amount of provisioned food consumed per animal relative to the amount offered per animal for ringtailed lemur troops on St. Catherines Island, 2002-2003. Proportion of provisioned chow consumed is listed above each bi-monthly time period. Proportion of provisioned fruit/veg consumed was consistently 0.10 throughout the study.



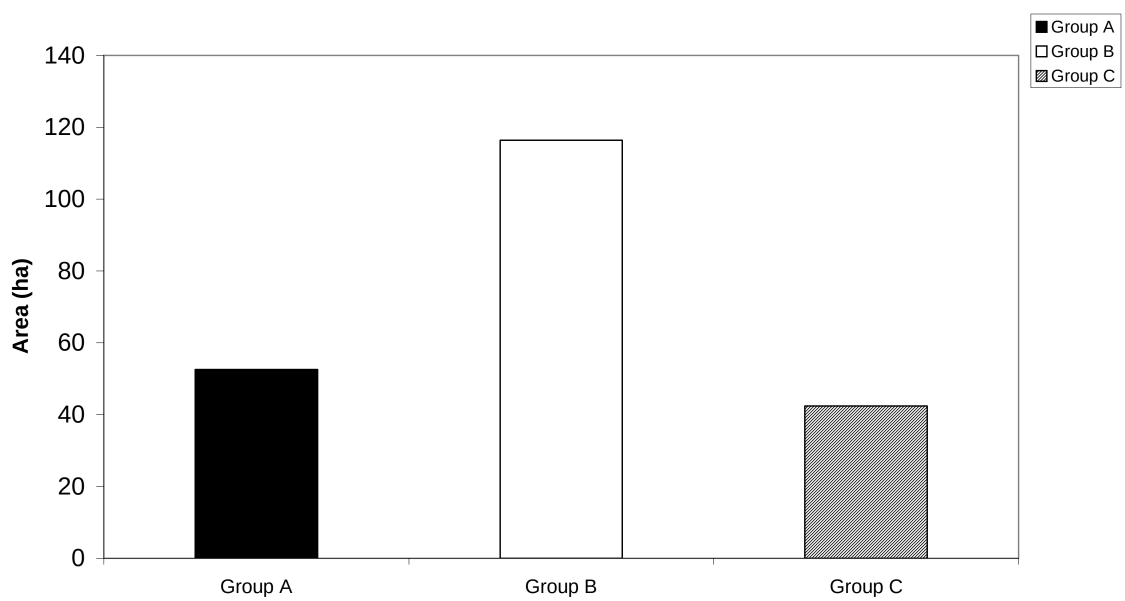


Figure 9. Home range sizes (ha) during each time period and total annual home range size for ringtailed lemur troops on St. Catherines Island, 2002-2003.

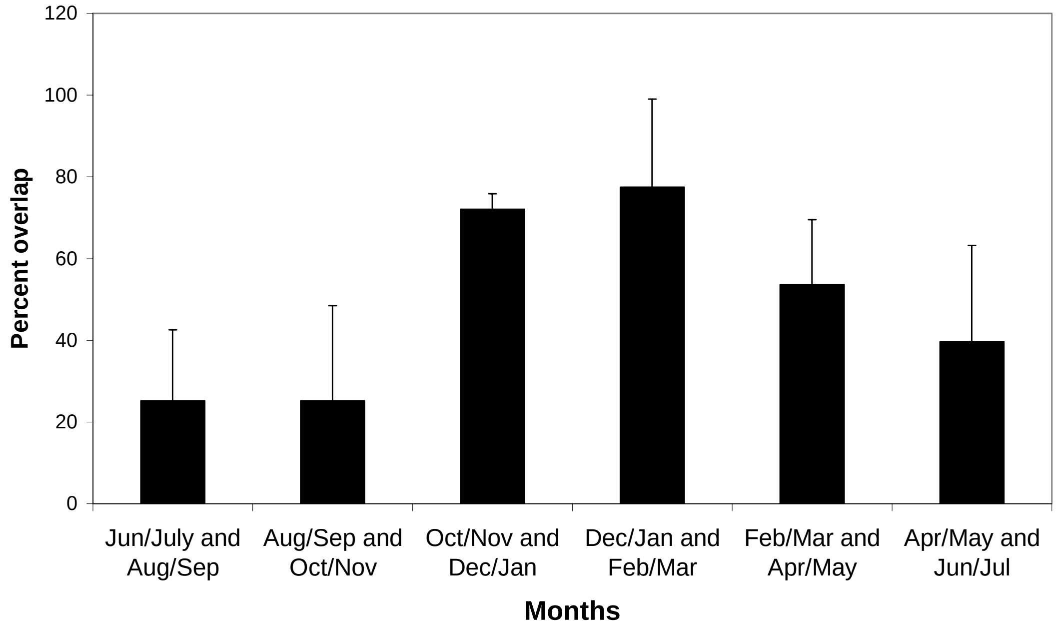


Figure 10. Percent of (mean +SE; n =3 groups) between home ranges from consecutive bi-monthly periods for ringtailed lemur troops on St. Catherines Island, 2002-2003. This percentage was calculated by determining the area (ha) for which consecutive bi-monthly home ranges overlapped and then dividing this area by the home range for the earlier bi-monthly time period.

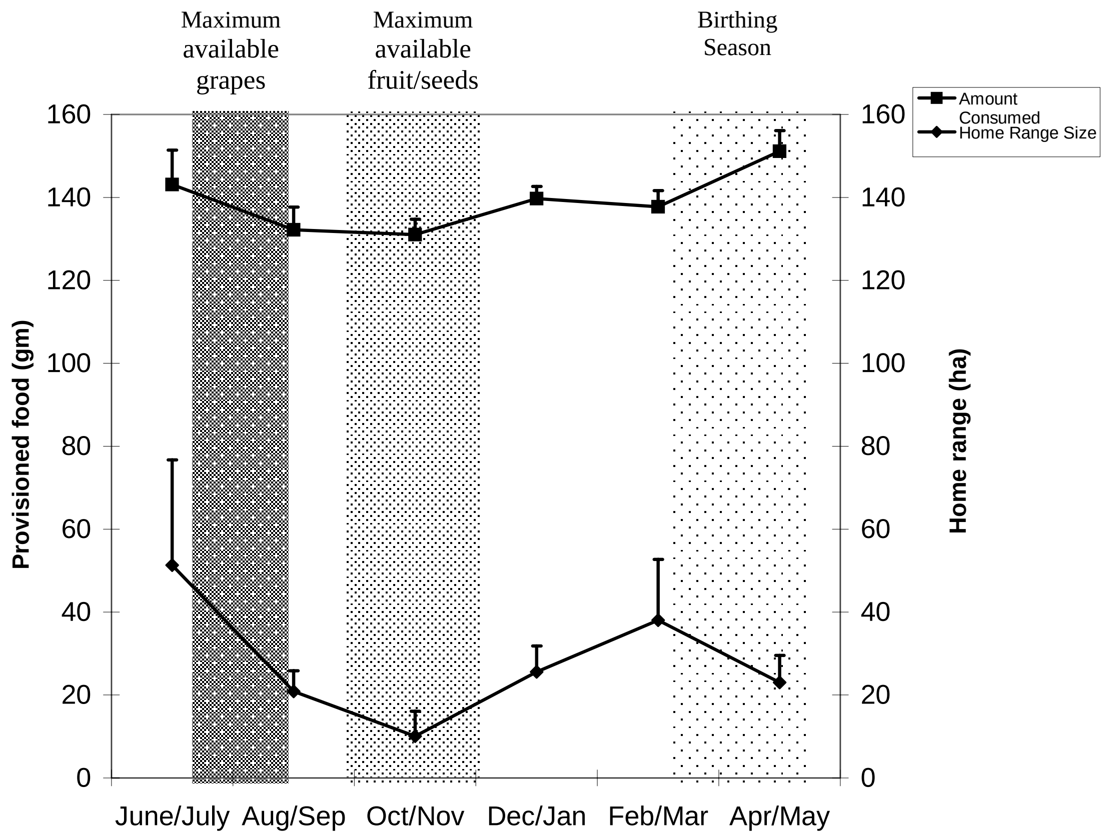


Figure 11. Relationship among home range (mean +SE), amount of provisions used (mean +SE), and food availability over the annual cycle for ringtailed lemur troops on St. Catherines Island 2002-2003.

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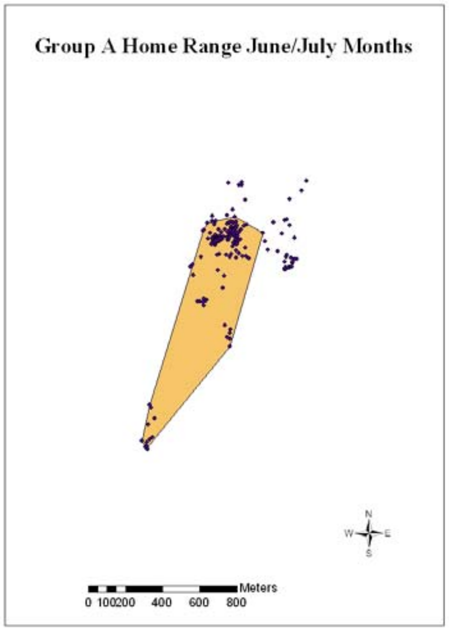
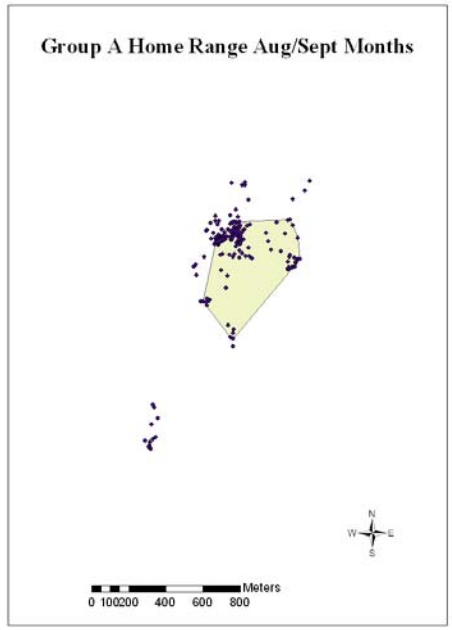
APPENDICES

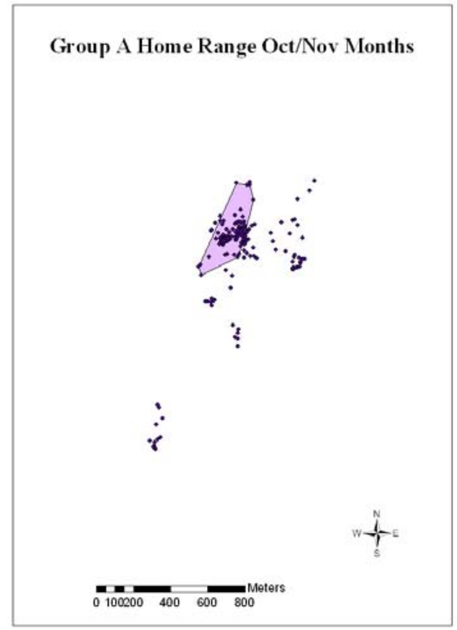
Appendix A, Maps 1-3. Group A Seasonal Home Range Maps. Maps show group ranging patterns for each bi-monthly time period and all GPS locations for Group A for the entire sampling period (July 2002 through July 2003).



Map 1



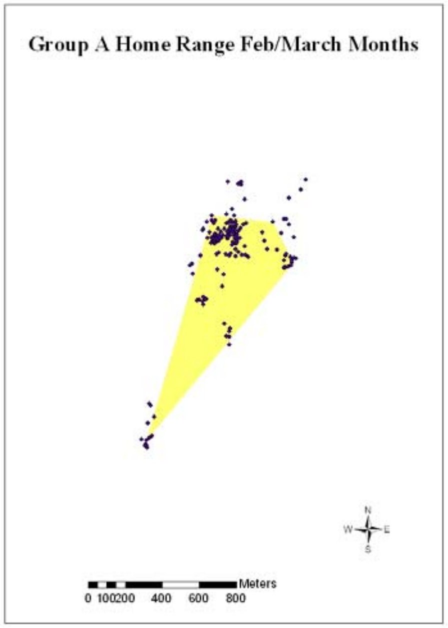
Map 2



Map 3

Appendix A, Maps 4-6. Group A Seasonal Home Range Maps. (continued)

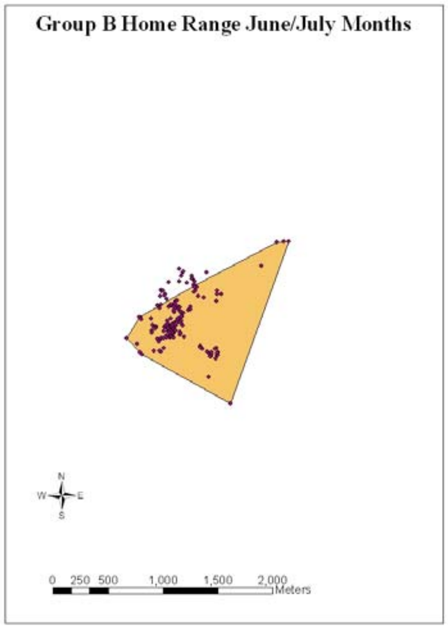
Map 4



Map 5

Map 6

Appendix B, Maps 1-3. Group B Seasonal Home Range Maps. Maps show group ranging patterns for each bi-monthly time period and all GPS locations for Group A for the entire sampling period (July 2002 through July 2003).



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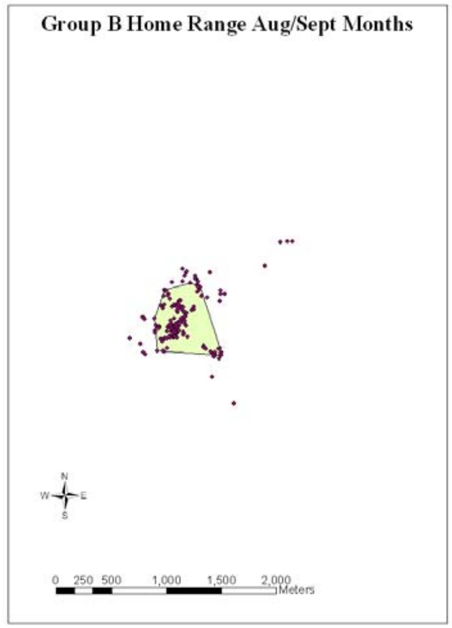

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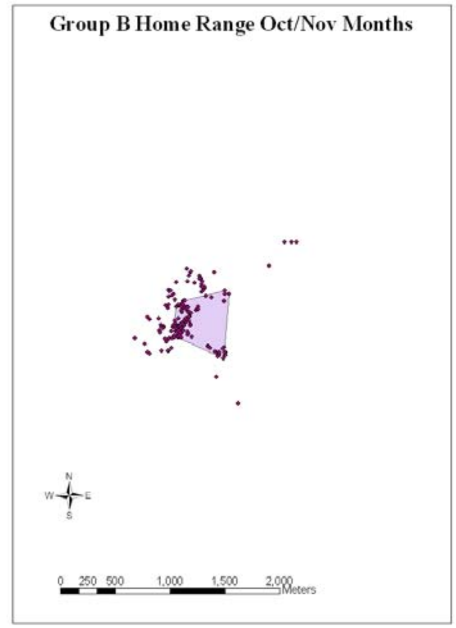
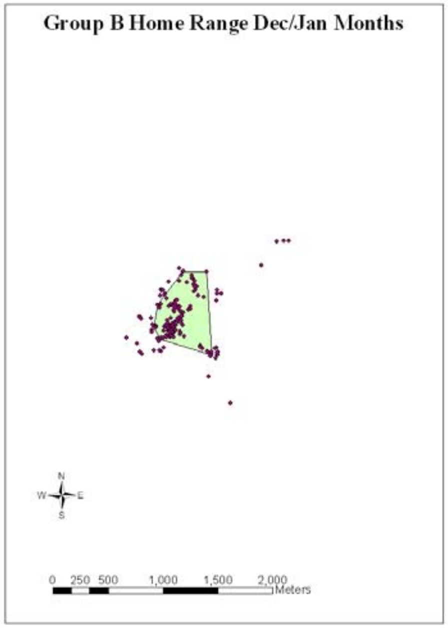


Map 3

Appendix B, Maps 4-6. Group B Seasonal Home Range Maps. (continued)



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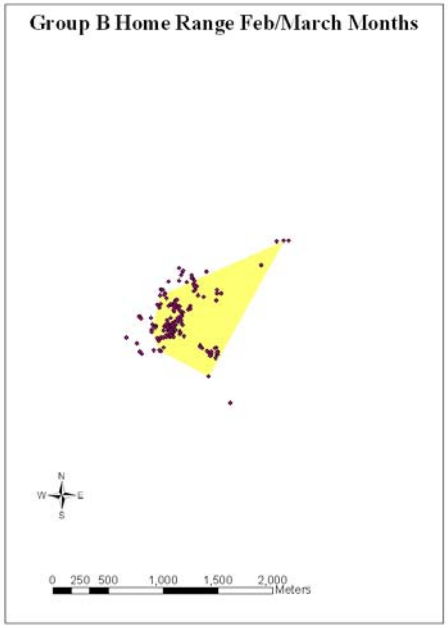

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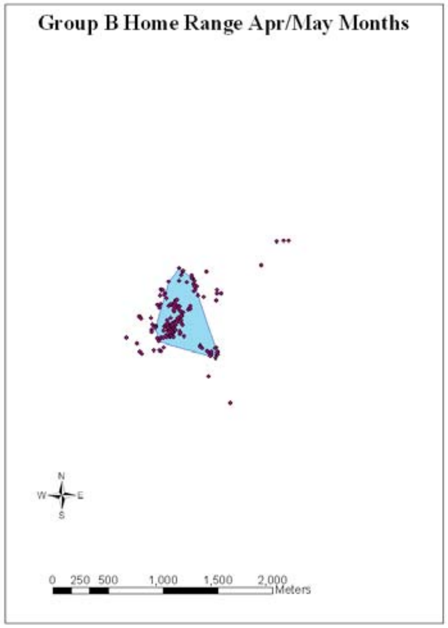
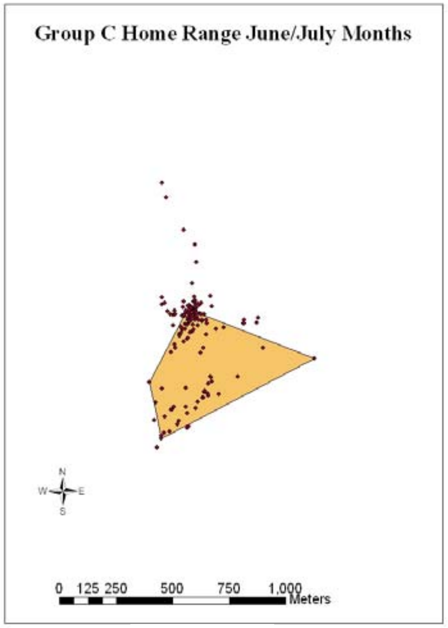
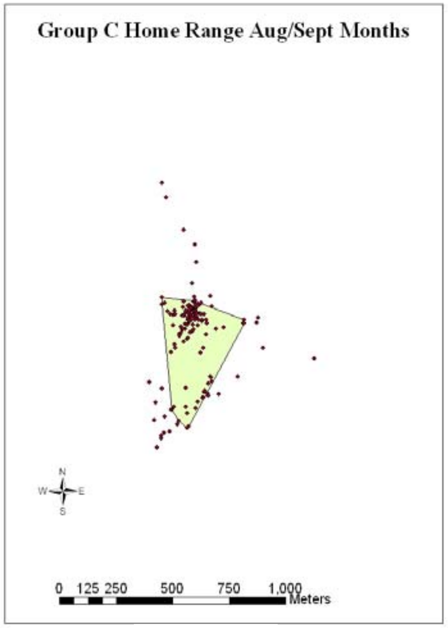


Map 6

Appendix C, Maps 1-3. Group C Seasonal Home Range Maps. Maps show group ranging patterns for each bi-monthly time period and all GPS locations for Group C for the entire sampling period (July 2002 through July 2003).



Map 1



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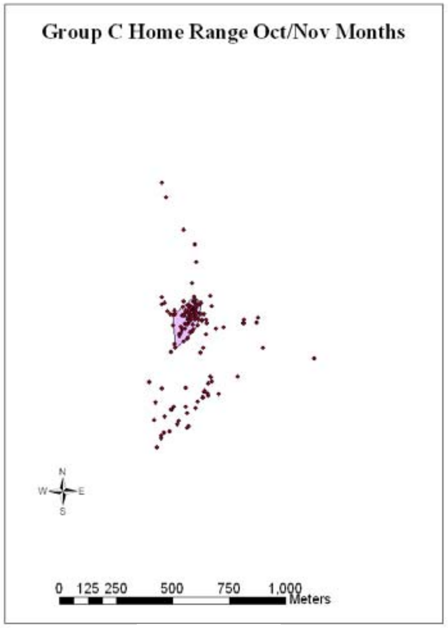
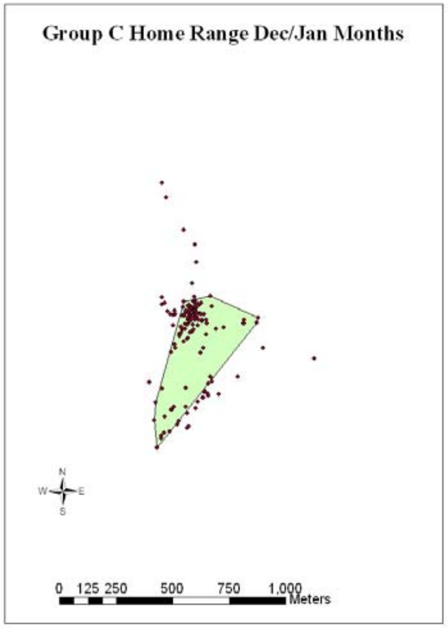


Map 3

Appendix C, Maps 4-6. Group C Seasonal Home Range Maps (continued)



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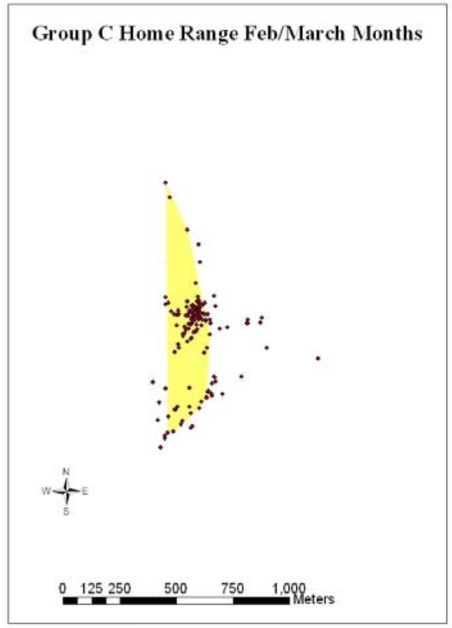
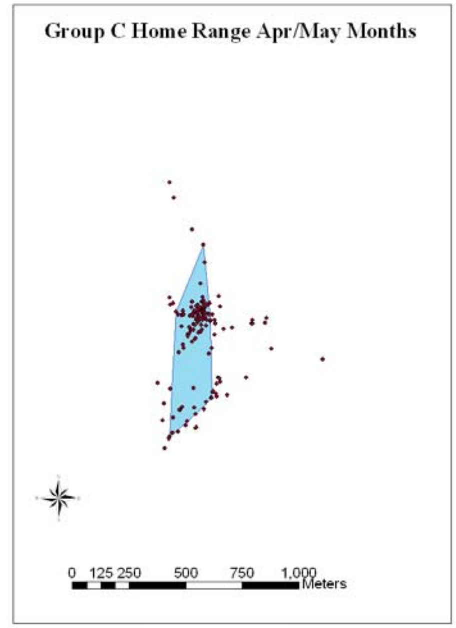


Map 5



Map 6