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Differences in behavior between captive and wild ring-tailed lemur (*Lemur catta*) populations: Implications for reintroduction and captive management

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Differences in behavior between captive and wild ring-tailed lemur (*Lemur catta*) populations: Implications for reintroductions and captive management

by

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A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of
MASTER OF ARTS

Major: Anthropology

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ABSTRACT

Part of the conservation strategy of zoos is participation in *ex situ* conservation efforts in the form of captive breeding programs. Standardizing methods to describe and quantify behavior of animals housed at different institutions is an essential tool for understanding intra-species behaviors [Carlstead 2000; Carlstead 2002]. The primary objective of this study was to determine if a significant difference exists between the behavior of captive and wild populations of *Lemur catta* (ring-tailed lemurs) and to explore the implications of the results for captive management and reintroduction programs. Captive lemurs were found to be more inactive than wild lemurs and the type of enclosure (indoor or outdoor) had an impact on their species-typical sunning behavior. Zoos have several options to promote and maintain species-specific behaviors in captive populations.

CHAPTER 1: INTRODUCTION

The history of the modern zoo stretches back over 200 years [Mullan and Marvin 1999]. Since that time, zoos have transformed from mere collections of exotic animals meant to amuse the public to leaders in education and conservation, visited by approximately 10% of the world's population annually [WAZA 1983]. Part of the conservation strategy of zoos is participation in *ex situ* conservation efforts in the form of captive breeding programs. The goal of *ex situ* programs is either to preserve species in captivity outside of the natural habitat, for eventual reintroduction into the wild or to prevent complete extinction [WAZA 2009].

Coordination of a global captive breeding program requires a set of guidelines for all participating institutions to follow. These guidelines should address issues such as genetic diversity, the avoidance of inbreeding, demographic stochasticity, psychological well-being and other health issues. At this time, there is no single set of captive breeding or reintroduction guidelines, as captive breeding guidelines are subsumed into reintroduction guidelines for specific species. The problem with this approach is that facilities participating in breeding programs with no intention to reintroduce (i.e. facilities that breed and sell or exchange individuals) may select for individuals that do well in captivity but are not suited for reintroduction. The consequences are that reintroductions, particularly those that involve primates, are frequently unsuccessful [Kleiman and Beck 1994].

One of the primary challenges of captive species management is assessing and coordinating husbandry protocols that facilitate the reproductive and behavioral potential of all individuals in the captive population [Carlstead 2000]. Standardizing

methods to describe and quantify behavior of animals housed at different institutions is an essential tool for understanding intra-species behaviors [Carlstead 2000; Carlstead 2002]. Determining how captivity alters the frequency and expression of species-specific behaviors is a component of building captive environments that balance the “artificial and restrictive characters on one side and the essentials of the animals’ natural environment on the other” [Hodges et al. 1995]. Assessing how captive populations differ from wild populations is only the first step in establishing the aforementioned balance, but it is one of the more challenging aspects of research in a zoological setting. The results of this study on ring-tailed lemurs indicate that such an undertaking is possible, although several methodological challenges still exist. Information acquired from the current study and similar research provide a valuable tool for captive animal managers, keepers, and reintroduction project managers that will aid in decision making processes that effect the lives of captive charges.

1.1 Objectives and Hypotheses

The primary objective of this study was to determine if a significant difference exists between the behavior of captive and wild populations of primates and to explore the implications of the results for captive management and reintroduction programs. A secondary objective was to use methodology employed in multi-institutional studies to determine which aspect(s) of the zoo environment results in the greatest behavioral departure from wild conspecifics and if the resulting variables

can be altered across all or most institutions to create a captive population of individuals that exhibits consistent frequencies of species-specific behaviors.

Using reintroduction as a goal can allow us to evaluate the quality of the captive environment, even if the specific individuals under study will not be reintroduced [Snowdon 1994]. Captive animals that are kept in conditions that promote the expression of species-specific behaviors with the same frequency as wild conspecifics are important to zoos, researchers, and the zoo-going public as sources of information. Additionally, these animals may one day be the stock from which we choose individuals to release into the wild. The importance of behavioral studies in conservation programs has gained ground over the last ten years [Angeloni et al. 2008; Singh and Kaumanns 2005; Sutherland 1998], but there is still a significant gap between captive and field studies. Methodological differences make it difficult to compare wild and captive populations, as do the confounding factors of captivity. This study did not seek to resolve those methodological challenges; instead, I sought to work within the limitations to produce meaningful results that can provide insight into the current state of a captive population when compared to wild conspecifics. It is necessary to continue to refine methodical limitations related to captive research in order to assist captive facilities and reintroduction project managers. Reintroduction protocols emphasize the need to use individuals from the captive population that are genetically and behavioral suited to the release site [Beck et al. 1987; Beck et al. 2007; Kleiman and Beck 1994]. It is difficult to determine which captive individuals are suited for release without first establishing what aspects of captivity must be manipulated to elicit wild behaviors. To encourage the

same level of behavioral diversity in captivity that characterizes wild populations, it is necessary to determine how different captive environments influence captive individuals. Establishing consistent monitoring protocols and compiling the resulting information allows researchers and managers to make informed decisions regarding the psychological and physical well-being of their charges [Watters et al. 2009].

In order to maximize the number of subjects available for study, I chose a common captive primate, *Lemur catta* (ring-tailed lemur), which is 'near threatened' in the wild [IUCN 2010]. The large number of captive individuals (approximately 3,000 in zoos and aquaria globally [ISIS 2011]) and comprehensive literature covering species-specific behaviors in the wild make this an ideal population to study. The ring-tailed lemur and other prosimians are excellent candidates for questions regarding the captive condition, as they have relatively short generation times (compared to anthropoid primates), which increases the chance that permanent behavioral changes as a result of captivity will become more widespread in the captive population in a shorter amount of time. Like many captive primates, ring-tailed lemurs are typically held in an environment that does not mimic all the qualities of the wild environment; therefore, they do not have the full spectrum of behavioral stimuli as wild ring-tailed lemurs [Hosey 2005; Tarou et al. 2005]. They are constrained by enclosures, and males are unable to disperse from their natal groups, as they do in the wild, unless transferred by their human managers. The animals do not make breeding choices freely – individuals are chosen for reproduction in order to promote genetic diversity in the captive population [AZA 2009b]. To this end, females and males are moved between institutions, potentially

upsetting existing social bonds and hierarchies. The presence of visitors also has a significant effect on captive animal behaviors as has the lack of natural stimuli [Hosey 2005; Myers 1978].

We do not necessarily expect to see a dramatically different catalog of behaviors when comparing captive and wild populations, but the expression of these behaviors may differ [Keith-Lucas et al. 1999]. The zoo visitor can see primates grooming, feeding, resting, or engaging in any number of species-specific behaviors. However, an animal under stress may overgroom themselves or others; limited access to foraging opportunities may reduce the amount of time spent looking for food; the lack of stimuli may result in more time spent inactive. I explore number of questions that aim to indentify variables that are most important to the expression of ring-tailed lemur species-specific behaviors. Do the type of enclosure (indoor/outdoor), human managed social groupings, and the presence of zoo visitors alter behaviors of captive ring-tailed lemurs when compared to wild conspecifics? Which of these variables present in captivity has a significant effect on the expression of behaviors? I address these questions using published information from wild studies and my own observations of captive lemurs.

Activity

Excessive inactivity in captive primates is a common problem in zoos and an issue that managers attempt to address with cage design, enrichment (food and non-food) and environmental stimuli [Dishman et al. 2009; Morgan and Tromborg 2007]. Wild ring-tailed lemurs spend over 50% of their time in inactive behaviors

such as resting and grooming [Jolly 1966a; Keith-Lucas et al. 1999]. The remainder of their time is spent engaged in active behaviors, such as foraging and traveling [Keith-Lucas et al. 1999]. Because captive animals do not have the same opportunity to engage in more active behaviors, we expect to see differences. However, activity level can be used to assess whether the captive environment provides levels of stimuli that encourage the expression of skills such as foraging and climbing. Lemurs in captivity do not have access to the same foraging and traveling opportunities as wild or free ranging groups. Therefore, it was predicted that 1) lemurs in captivity would spend significantly more time inactive than wild lemurs. However, assessing inactivity level in conjunction with certain species-specific behaviors provides a more complete assessment of captive lemur behavior. In ring-tailed lemurs, sunning is one such behavior.

Sunning

Sunning behavior has been documented in both wild and captive populations of lemurs [Jolly 1966a; Keith-Lucas et al. 1999; Law 2008]. Lemurs will climb to the upper branches of an east-facing tree in the morning and warm themselves in the sun (Figure 1.1). This behavior is found in all wild populations and is important for its thermoregulatory function and, as the best example of lemur species-specific behavior (found in *Lemur catta*, *Propithecus spp* and *Varecia variegata*) it is not found in other non-Lemuroid primates in this particular form. Although captive lemurs may not need to sun due to climate-controlled environments, the absence of this behavior may indicate that the lemurs have no exposure to natural stimuli and may

not engage in other species-specific behaviors. Outdoor lemur enclosures may not allow exposure to early morning sun, and indoor enclosures may not have adequate sunlight to elicit frequent occurrences of sunning. Indoor enclosures are temperature controlled using centralized heating or heat lamps. In this situation, sunning no longer serves a thermoregulatory function and therefore we would expect that 1) lemurs in captivity will spend less time sunning than wild lemurs and 2) lemurs housed in indoor enclosure will spend less time sunning than those housed outdoors. Sunning is understudied in lemurs, but it is known to serve an important function for reducing the cost of thermogenesis and to help control ectoparasites [Loudon et al. 2006; Pereira et al. 1999]. Although not referred to in the lemur literature as a programmed behavior, it can be argued that sunning has a genetic component (regulation of temperature) and a learned component (appropriate sunning locations, posture). Two formerly captive ring-tailed lemurs released into St. Catherine's Island free-ranging colony displayed abnormal sunning behavior after release. These individuals, apparently disoriented by their new surrounding, were observed to assume a sunning position while sitting in the shade with their backs to the sun [Keith-Lucas et al. 1999].



Figure 1.1 Sunning adult male lemur (Little Boy) at Blank Park Zoo

Social Structure

Social structure and, to some degree, social behavior in primates is affected by phylogeny [Spuhler and Jorde 1975]. Ring-tailed lemurs have been noted to have social systems that more closely resemble haplorrhine primates than other strepsirrhine primates [Jolly 1966]. Their relatively more complex social systems may result in the ability to be more adept at reading social cues that dictate competition for resources [Sandel *et al.* 2011]. Therefore, social structure and

behavior have a significant impact on the psychological and physical wellbeing of captive primates, as demonstrated by decades of research on maternal deprivation and isolation in primates [Latham and Mason 2008]. While the modern zoo does not habitually keep individuals in isolation, abnormal social conditions may have a significant impact on the physical and psychological well being of the animals.

Wild lemurs are found in multi-male, multi-female groups that average 13 individuals (range 5-27 individuals), with a male to female ratio of 1:1 [Jolly 1966a; Sauther et al. 1999]. These groups are female dominated, centering on adult females and their offspring, which typically come from several matrilineal lines [Sauther et al. 1999]. More closely related individuals engage in less aggressive behaviors than those more distantly related [Sauther and Sussman 1993]. Social groups in captivity are artificially managed to meet the requirements of breeding programs, and individuals are frequently transferred between institutions [AZA 2009b; Villiers 2007; Villiers 2009]. Based on the natural social structure and behavior of ring-tailed lemurs, I hypothesized that 1) lemurs housed in primarily male or primarily female groupings would engage in more frequent agonistic interactions than wild populations and 2) unrelated individuals would engage in higher rates of aggression than related individuals in the group.

Visitors

Studies on various primate species have shown that zoo visitors are a source of stress for captive primates [Carlstead 1996 (mammals); Hosey 2005 (primates); Wood 1998 (*Pan troglodytes*)]. The presence of visitors can have a significant

influence on the initiation of stereotypical behaviors, which are abnormal repetitive behaviors that lack any goal or function [Garner 2005; Hosey 2005]. Surveys of captive prosimians have shown that animals housed in indoor enclosures engage in abnormal and stereotypical behaviors (pacing, somersaulting, overgrooming, and self-injurious behavior) more frequently than those housed outside [Hosey 2005; Tarou et al. 2005]. I hypothesized that 1) lemurs that have more visitors to their enclosure would be observed engaging in more stereotypical behaviors, and 2) lemurs housed indoors would engage in these behaviors more often.

1.2 Background and Significance

Ring-tailed lemurs provide an example of a captive primate that is a likely candidate for reintroduction to the wild. As stated above, they are common in captivity worldwide. Among primates, lemurs are thought to rely relatively less on learned behaviors [Jolly 1966b; Kendal et al. 2010]. However, while their conservation status indicates reintroduction to the wild should be considered, the reasons for their decline may preclude such an eventuality. Sussman *et al.* [2006], for example, estimate that between the 1985 and 2000, 9.5% of ring-tailed lemur habitat was destroyed. The current IUCN Red List classification of the species is 'Near Threatened', and their numbers are decreasing in the wild, primarily due to habitat loss and hunting [IUCN 2010]. A political coup in Madagascar in 2009 and the resulting political and social instability have increased the rates of deforestation, both in and out of protected areas, further threatening the future of ring-tailed and other lemur species [Bearak 2010; Iloniana 2011]. Regardless of the apparently

bleak circumstances for wild primates currently, a major goal of today's zoos is to serve as a potential reservoir for individuals of species in danger of extinction, and they attempt to manage these species under circumstances that elicit natural behaviors should reintroduction be a viable step.

In a zoo setting, exhibit designers and keepers manufacture enclosures that mimic the wild but, despite best efforts, cannot replicate a completely natural environment in captivity. Wild animals will manipulate their environment to search for food, water, and sometimes just to explore. For example, grizzly bears (*Ursus arctos horribilis*) in the wild will move rocks and logs to search for food, stand up to examine and paw at bee and bird nests, and fish in pools and streams [Myers 1978]. Reinforcement of these behaviors comes from success at finding food. If they are continually unsuccessful at finding food under a log, they will stop looking [Myers 1978]. Given the choice of food offered *ad libitum* and food gained through a task, captive gibbons (*Hylobates lar*) will work for their food, underscoring the importance of stimuli in captive environments [Markowitz 1975]. For primates, it is also essential that we meet psychological needs as well as physical ones. Cognitive needs and species-typical behavioral repertoires are not always met or prompted by captive conditions, resulting in stereotypical behaviors, disturbed functions, and loss of species-specific behaviors [Van Hooff 1986]. Meeting these needs is our ethical responsibility as caretakers, and it provides the animals the opportunity to express the social and cognitive skill sets that are found in the wild.

The captive environment should offer the cues appropriate to encourage the entire behavioral potential of an animal. This includes providing appropriate social

conditions, which for primate species play a particularly important role. Primates living in groups have a set of cognitive capabilities and “emotional dispositions” [Van Hooff 1986] that optimizes their inclusive fitness. Artificial social systems, such as those found in captivity, are less complex than those in the wild and may not provide adequate social interactions. Creating social groups and providing housing that allows the expression of natural social behaviors is essential to maintaining these behaviors, which can in turn increase the physical and psychological well-being of the animals [Rabin 2003]. This can also facilitate learning through interaction with conspecifics [West and King 1994].

The complex web of factors that stimulate the expression of species-specific behaviors makes it difficult to establish a clear understanding of how captivity alters wild behaviors. Reintroduction programs have demonstrated that a wide variety of behaviors can be lost over time, such as the ability to navigate effectively through a complex, three-dimensional arboreal environment [Kleiman and Rylands 2002]. If husbandry and management protocols are altered to incorporate natural behavior management (NBM) programs, as proposed by Rabin [2003], it may prevent the loss of species-specific behaviors in captivity. These programs are designed to elicit a natural behavioral response, as discussed above, and therefore maintain behavior crucial for survival in the wild. NBM programs hold great promise for captive breeding and reintroduction programs. Maintaining species as “wild” as possible while in captivity could reduce the amount of time and funding needed for reintroduction programs and increase the survivorship of reintroduced individuals. The effectiveness of programs like this requires multi-zoo cooperation in the

establishment and implementation of behavioral protocols. This relies, in turn, on understanding how captive animals behave in comparison to their wild counterparts [Hosey 2005].

CHAPTER 2: LITERATURE REVIEW

There is extensive literature addressing captive behaviors in primates (see Hosey [2005] and Melfi [2005] for overviews) but very few multi-zoo studies that explore how captive populations differ from their wild counterparts [Mellen 1994; Mitchell and Hosey 2005; Ryder 1995; Shepherdson and Carlstead 2001]. Comparisons between zoos are difficult due to the differences between institutions. These include, but are not limited to: husbandry practices including feeding schedules, animal movement, and training; the number of visitors; the type and quality of the enclosure; type and quality of enrichment; generations in captivity; and the social structure of the group. Most commonly, the number of visitors and effects of environmental enrichment are the focus of behavior based zoo studies [Mitchell and Hosey 2005]. These studies give valuable insight into how particular factors of captivity alter behavior but do little to determine how captivity changes the behavioral suites of a given species.

Much of the existing literature on captive *Lemur catta* stems from studies of free ranging colonies on St. Catherine's Island and the Duke University Primate Center [Keith-Lucas et al. 1999; Wright 2008]. The lemurs housed at St. Catherine's Island range freely, feeding on growing vegetation and a provisioned diet [Parga and Lessnau 2005]. Lemur colonies at Duke University are housed in both free ranging areas and in traditional cage-type enclosures. Few studies focus solely on the activity budget and behaviors of captive *L. catta* [Baracco et al. 2009; Dishman et al. 2009; Law 2008; Tarou et al. 2005]. However, existing research suggests that in a zoo environment they exhibit abnormal (e.g., stereotypical) behaviors but will

increase activity levels in response to feeding enrichment [Dishman et al. 2009; Tarou et al. 2005].

2.1 Captive Breeding and Reintroduction for Conservation

Captive breeding for conservation is often referred to as the Ark Concept [Bowkett 2009; Tudge 1992]. Tudge [1992] outlined the task of captive breeding for conservation as keeping “as many species as possible alive in captivity for as long as is necessary (which could well mean several centuries) in a state in which they are capable of returning to the wild” (p 61). Captive breeding for conservation purposes is an incredibly complex undertaking and, for some, a misguided effort due to the limited success and high cost [Snyder et al. 1996]. Proponents of captive breeding programs acknowledge the challenges of such efforts but feel that in the current biodiversity crisis, it is a valuable undertaking and in some cases, the only way to ensure the future of some species.

Reintroduction is defined as “the process of re-establishing a population of animals within the area of its original wild habitat” [Brambell 1977]. The underlying concept of reintroduction is that the original habitat molded the gene pool of the natural population [Brambell 1977]. Therefore, although the original selective pressures may change over time through anthropogenic habitat modification, species are best suited for the habitat in which they evolved. In recent years, reintroduction is appearing in the literature as a type of restoration along with translocation, introduction, and augmentation (restocking) [Morrison 2009].

Captive breeding – the early years

Early collections of wild animals in captivity were typically in the hands of private, wealthy individuals and seen as source of amusement. [Hosey et al. 2009]. The earliest records of these menageries dates back to 2,5000 BC in Egypt and China, and the tradition continued in Europe through the late 18th century, when zoological gardens began to appear in France, England, and Germany [Hosey et al. 2009]. Any breeding that occurred was a by-product of putting together individuals that could cope with the stresses of captive and reproduce. One of the earliest attempts at captive breeding for conservation occurred at the end of the end of the 19th century. The last 18 Père David's deer (*Elaphurus davidianus*) were gathered from private collections in the United Kingdom, France and Germany to form a breeding colony in England [Jiang and Harris 2008]. Extirpated from their native China in 1900, only 11 of the last 18 individuals were reproductively active and despite potential for genetic bottlenecking, the herd reached 250 individuals by 1945 [Jiang et al. 2000]. Reintroduction to the historical range in China began in the mid 1980s with 37 individuals, and the population now consists of well over 1,000 stable (albeit not genetically diverse) individuals [Yan 2007].

Despite this early success, true coordinated efforts of captive breeding for conservation did begin to appear until the middle of the last century as zoo and collection managers began to realize that animals were becoming rare in the wild. Increased rarity meant that replenishing the captive stock was no longer as simple as placing an order with a dealer and receiving a shipment of elephants. In order to maintain their captive populations, zoos would have to begin breeding programs

[Tongren 1985]. Initially undertaken as a way to ensure a constant stock of animals to exhibit, captive breeding was quickly adapted as a means of conservation. The Jersey Wildlife Preservation Trust, established in 1963 was the first organization dedicated to controlled captive breeding programs for conservation [Durrell 1972]. In 1972, the first World Conference on Breeding Endangered Species in Captivity as an Aid to Survival was held at the Jersey Zoo, the headquarters of the Jersey Wildlife Preservation Trust [Martin 1975]. Early *ex situ* conservation efforts reported at the conference included reptiles, a variety of birds, and a small selection of mammals. Among the reports were early reintroduction efforts involving giant tortoises, Hawaiian geese, Przewalski wild horses, and the Arabian oryx, signifying the incorporation of reintroduction into captive breeding goals early on.

Ex situ conservation

Conservation biology is a relatively young discipline, born from the need to rapidly assess problems and propose and/or implement solutions before all the facts are known [Meine et al. 2006; Soulé 1985]. In short, conservation biologists are crisis managers, and must act quickly to protect species from extinction. *In situ* conservation efforts are at the forefront of extinction protection, considered by many to be the best approach for species conservation [Keller et al. 2002; Ryder 1995; Snyder et al. 1996]. By maintaining and/or expanding existing habitat, we can minimize the disruption to species and involve local communities to ensure long-term survival. However, changes can occur that disrupt years of on site conservation work and put animals back on the path to extinction (e.g. socio-political upheaval, as

in the Democratic Republic of Congo and Madagascar [Bearak 2010; Iloniana 2011; Jenkins 2008] or the World Bank withdrawing funds from the Tana River Primate National Reserve [Mborra and Butynski 2007]). Unfortunately, we cannot predict when or where these events may happen, and it becomes necessary to turn to other conservation programs.

Ex situ efforts, such as captive breeding and reintroduction have been termed as extinction insurance, and viewed as such are complimentary to (not replacement for) *in situ* conservation [CBD 2011; Keller et al. 2002; Tudge 1992]. Maintaining populations outside of their natural ranges insulates species from factors causing decline in their wild counterparts. There are distinct advantages to *ex situ* conservation, but the approach does have its limitations [Snyder et al. 1996; Snyder et al. 1997]. The number of factors that must be taken into account to successfully reintroduce captive bred populations currently restricts its application to conservation projects, but it does hold promise for the future. The success of this approach depends on determining what contributes to success and how to best apply new and existing techniques to upcoming programs. Relevant factors include both biological (carrying capacity, extinction probability, the origin of founders, etc) and non-biological components (administration, long term funding, technical advice, etc), as well as an areas where the two intersect (public support, socio-economic environment, population management and monitoring [Stanley Price 1991]. Captive breeding for the purpose of preservation continues to be part of the conservation planning of zoos worldwide and, by combining the efforts of zoos and researchers, it is possible to establish a mechanism that will more readily promote successful

reintroductions [Bowkett 2009; Kleiman 1989; Rabin 2003]. The long life histories, high degree of social learning and complex behavioral patterns make primates a particularly challenging taxon to reintroduce [Lonsdorf 2007]. However, by increasing our understanding of how captive populations differ from wild populations, captive breeding and reintroduction can become important conservation strategies.

2.2 *Lemur catta*

Lemur catta are small primates found on the island of Madagascar. Ring-tailed lemurs live in social groups consisting of multi-male/multi-female groups that are focused around a single dominant female, although adult sex ratios are usually 1:1 [Jolly 1966a]. The average group size is 13 individuals but can range between 5-27 [Jolly 1966a; Sauther et al. 1999]. Females stay within their natal groups, and males disperse [Jolly 1966a]. The species is not considered territorial in a strict sense, but they will defend seasonal resources against other ring-tailed lemur troops [Sauther and Sussman 1993]. They are diurnal and more terrestrial than other lemur species [Jolly 1966a]. Patchily distributed throughout the southern part of the island of Madagascar their diet consists of fruit, leaves, stems, flowers, and insects [Sauther et al. 1999]. They are endemic to Madagascar and are currently classified by the IUCN as Near Threatened [IUCN 2010].

Males and females are minimally dimorphic; males can be easily identified by their hairless black scrotums and appear slightly larger in the head, upper arms, and shoulders. Males have well-developed wrist and brachial glands and both sexes utilize anogenital glands for scent marking [Cawthon Lang 2005]. Characterized by

light gray fur and a black and white face mask, the most striking feature of *Lemur catta* is the long black and white ringed tail for which it is named. Jolly [1966a] described her first impression of a troop of ring-tails as “a series of tails dangling straight down among the branches like enormous fuzzy striped caterpillars.” The tails function in stink-fights during which the tail is anointed with the wrist and brachial glands and then waved at the offending individual [Gould et al. 2003]. The stink fight underscores the importance of olfactory and visual communication for ring-tailed lemurs. The male wrist glands have a spur that is used to scratch the surface of trees or branches, thus leaving both a visual and odor cue for conspecifics [Gould et al. 2003; Jolly 1966a].

Gregarious and playful, ring-tailed lemurs have a broad vocal repertoire that is similar to Old World monkeys [Jolly 1966a; Sauther et al. 1999]. Vocalizations include purrs and faint clicks during mutual grooming sessions, yips that accompany aggressive interactions, and contact mews during traveling [Jolly 1966a]. It is common for one individual to begin vocalizing and have other members of the troop respond with a contact call or to have contact calls given when sighting a familiar human [Jolly 1966a].

Ring-tailed lemurs spend a majority of their time sleeping, sunbathing and resting, with males engaging in these activities slightly more than females [Rasamimanana et al. 2006]. The remainder of their time is spent feeding, moving, traveling, and grooming. Activity budgets presented in the literature vary (Table 2.1). The breeding season is brief, occurring during a one to three week period in April and females give birth to single offspring in August; captive populations in the

Northern Hemisphere experience a 6-month shift in timing [Gould et al. 2003; Jolly 1966a; Parga and Lessnau 2005]. Wild *Lemur catta* live in female-resident multi-male/multi-female groups that are focused around resident females and their offspring [Sauther and Sussman 1993]. Groups contain multiple matriline, and one single matriline is not dominant to others, although this has been observed in captive free-ranging groups [Sauther and Sussman 1993]. Adult males begin to disperse from their natal groups at age three and repeat their migration once every 3.5 years, on average [Sussman 1992]. Adult females are dominant to males, but one male will typically have priority access to females and food [Jolly 1966a; Sauther and Sussman 1993].

	Berenty Reserve [Jolly 1966a]	Antserananomby [Keith-Lucas et al. 1999]	St. Catherine's Island [Keith-Lucas et al. 1999]
Foraging	31%	25%	26%
Resting and Grooming	50%	46%	55%
Traveling	13%	19%	19%
Other	6%	10%	-

Table 2.1. Activity budgets of wild and captive free ranging *Lemur catta*

Review of the literature did not reveal any studies that have constructed a complete activity budget using the categories in Table 2.1 (foraging, traveling,

resting, grooming, and other) although these categories are commonly used in studies of wild lemurs. Releases of captive lemurs into the free ranging (provisioned) St. Catherine's island population resulted in lowered body weight, an increase in general activity, ranging and foraging (and associated decrease in eating provisioned food) [Keith-Lucas et al. 1999], suggesting that captive lemurs do not spend as much time engaging in these behaviors as their free ranging or wild counterparts.

Captive *Lemur catta* housed in zoos accredited by the Association of Zoos and Aquariums are managed under the AZA Species Survival Plan (SSP). The overall goal of these plans is to use captive populations to ensure demographic stability and genetic diversity of a species that is threatened or endangered in the wild through breeding and management recommendations [AZA 2009b]. The 2009 update to the *Lemur catta* SSP estimates the captive population in AZA accredited institutions to be 504 specimens, exceeding the Prosimian Taxon Advisory Group recommendation of 475 individuals [Villiers 2009]. Pedigrees are tracked with a species studbook, which lists all known life history information for an individual (sire, dam, place of birth, transfer, and rearing conditions) [Villiers 2007]. The focus on conservation of genetic diversity does not address the need for an environment that stimulates behavior. Maintenance of a genetically diverse population is part of a more holistic approach to captive management – an approach that should also include guidelines for behavioral stability and conservation.

CHAPTER 3: METHODOLOGY

I studied captive ring-tailed lemurs at two different zoos in order to explore how the captive environment alters the behavior of this species. The behaviors chosen for inclusion in this study were all easily observable in the particular captive environments at each of the study sites. The frequency and duration of the expression of these behaviors indicate whether the captive environment is providing appropriate stimuli, both environmental and social, and minimizing the level of stress, as measured by stereotypical and agonistic behavior.

3.1 Subjects and Study Sites

This study was conducted on two groups of captive ring-tailed lemurs housed in zoological parks in the United States. One group of four lemurs was studied at the Blank Park Zoo (BPZ), located in Des Moines, Iowa. The second study group was housed at the Minnesota Zoo, approximately 30 miles south of Minneapolis, Minnesota in Apple Valley. The BPZ lemur troop consisted of three males and one female. Table 3.1 summarizes information about the troop, including names, identification numbers (both institution and studbook), birth date, age at the time of study, and the characteristics used to identify the individuals. During the first days of data collection, names were assigned to the males based on physical characteristics to facilitate individual identification. The three males were transferred to BPZ from the Washington Park Zoological Garden in Michigan City, Indiana in June of 2002.

Name	I.D. (AZA)	I.D. (Zoo)	Birth Year	Age (yrs)	Kin Relations	Physical Characteristics
Rafiki (F)	3294	1821	2001	9	None	Female, large mammarys
Old Man	3075	1473	1987	23	Sire of Little Boy & Scarface	Loose skin around belly, muddled mask, scruffy fur
Little Boy	3092	1475	2000	10	Offspring of Old Man	Smallest male, pointy snout, defined mask
Scarface	3088	1474	1998	12	Offspring of Old Man	Scar on side of nose

Table 3.1 Description of lemurs at Blank Park Zoo

The oldest male is the sire of the two younger males, but his origin and lineage are unknown, as is the lineage of the young males' dam. The younger males are known to be parent reared, but the rearing situation of their sire is unknown. The female, initially obtained by the Indianapolis Zoo from a private collection, was transferred to BPZ in October of 2006. She was hand reared by humans, and zoo personnel believe that she may have been a pet, but this cannot be confirmed. The group has non-breeding status, per the recommendations of the current ring-tailed lemur SSP, and the female has an IUD (intrauterine device) in place to prevent pregnancy. Lemurs in the Northern Hemisphere typically enter estrus 6 months out of phase with wild lemurs on Madagascar [Rasmussen 1985]. Therefore Rafiki would have

been expected to enter estrus during the observational period. She was not observed to have any estrus swelling or other indicators that she was cycling.

The BPZ lemur exhibit consists of an outdoor area for display during the hours the zoo is open, as well as indoor housing, where the lemurs are housed when the zoo is closed. Weather permitting, the lemurs are moved into the outdoor exhibit shortly before the zoo opens and moved back inside shortly after the zoo closes. For this study, zoo hours were 1000-1600 hours during October, and 1000-1500 hours for November collection dates. The exhibit is an elongated hexagon enclosed in wire. It is 40 feet long, 25 feet wide and narrows to 10 feet at the ends, providing the lemurs with ample space for both terrestrial locomotion. The sides are 15 feet tall and allow the lemurs enough height and purchase for climbing. Although the exhibit is not naturalistic in the strictest sense, it does contain grass, rocks, a small freshwater holding pond, small trees, and wild grape (*Vitis riparia*) vines (Figure 3.1). The vines grow along the sides and the roof of the cage, and there are several trees, including ash (*Fraxinus sp*), pawpaw (*Asimina triloba*), and sugar maple (*Acer saccharum*) that can be accessed from inside the cage; the lemurs are able to climb the cage to access these items. A gap filled with vegetation approximately one meter wide and a small fence approximately one meter high serves as a barrier between the lemurs and visitors. In addition to natural foliage, the lemurs are provided a total of 21 Purina Monkey Chow biscuits and 10 grams of spinach, and 90 grams each of carrots, bananas, and oranges. These items are spread in the outdoor enclosure each morning. During the study, the lemurs were seen to browse on wild grape leaves, as well as on the fallen leaves from surrounding trees and weedy species

growing in the exhibit. In addition to the food provided, occasional enrichment was given to the lemurs. This included items containing special treats such as peanut butter smeared onto plastic toys suspended from the trees, requiring the lemurs to actively manipulate the object for the treat (Figure 3.2)



Figure 3.1 Enclosure at Blank Park Zoo



Figure 3.2 BPZ enrichment. The item on the left contained peanut butter and the one to right contained fruit

The lemurs are held indoors when the zoo is closed and during inclement weather. Zoo protocol dictates that the lemurs are provided access to the indoor and outdoor enclosures during open hours when the temperature is below 18° C and above 1.5° C, and during heavy rain. They are denied access to the indoor enclosure when temperatures are above this range and kept indoors when temperatures fall below 1.5° C. The building consists of three small, interconnected rooms that contain shelves, nest boxes, and climbing surfaces. The lemurs are fed the same diet while indoors as they are given when outdoors. However, the food is presented to them in dishes indoors as opposed to scattered about for them to find.

Name	I.D. (AZA)	I.D. (Zoo)	Birth Year	Age(yrs)	Kin Relations	Physical Characteristics
Ursula (F)	2085	11056	1990	20	Dam of Lisa & Elizabeth	Middle finger of right hand sticks out; tail tapered
Lisa (F)	2469	11057	1994	16	Offspring of Ursula	Middle finger of left hands sticks up; amputated 4 th finger on left hand
Elizabeth (F)	2824	11058	1998	12	Offspring of Ursula	Short, blunt tail; visible dot on forehead
Amanda (F)	3050	11059	2001	9	Unrelated	Droopy eyelids; full, long tail
Oliver (M)	2677	12316	1996	14	Unrelated	Large, square head; clear mask; light eyes; darker coat

Table 3.2 Description of lemurs at Minnesota Zoo

At the Minnesota Zoo (MNZ), there are five adult ring-tailed lemurs. The group contains four females and one castrated male. The oldest female is the dam of two of the females. The youngest female is unrelated to the others, as is the male. At the start of the study, names and identifying features were provided by the zoo staff, so these characteristics were used throughout the study, as outlined in Table 3.2, along with ID numbers, kin relationships, birth date and age. All four females were born on St. Catherine's Island, Georgia, a semi-captive facility that contains several groups of free-ranging lemurs. The four females were transferred together from St. Catherine's Island to the Caldwell Zoo in Tyler, TX in 2001 and then to the Minnesota Zoo in 2003. The male was born at Dreher Park Zoo in West Palm Beach, FL and transferred to Binder Park Zoo in Battle Creek, MI at the age of one year. Eight months later, he was transferred to Kansas City Zoo in Kansas City, MO where he remained for four years, at which point he was moved to the Cleveland Zoo in Cleveland, OH. The Cleveland Zoo held him for six years before he was added to the troop in Minnesota. All of the lemurs in the Minnesota troop are parent raised, but none are recommended for breeding by the current SSP.

The lemur exhibit at the MNZ is along the Tropics Trail, a large indoor building that walks visitors through the tropical areas of the world region by region. 'Madagascar' is the first area that visitors enter, and the lemur exhibit is one of the first that is seen. The ring-tailed lemurs are exhibited with three red-ruffed lemurs (*Varecia rubra*) but do not share an evening holding area with them. The lemur area is surrounded at the base by mesh screening, which the animals are unable to climb. However, the screening near the middle and top of the enclosure provides a

climbing surface. In the center of the exhibit is a large tree structure with several cement branches that provide platforms for resting and sitting (Figure 3.3). These platforms are located at viewing height for the visitors. Several medium and small branches extend across the exhibit for climbing. The bottom of the exhibit consists of a small dirt area. Directly below the viewing platform is a shallow moat where the lemurs access the doors that lead to off-exhibit housing. Rock-like structures are found mid-way up the back and side walls of the exhibit. Much of the surfaces of these rocks are obscured by plantings, thus providing an area where the lemurs cannot be seen from the main viewing area.



Figure 3.3 The enclosure and viewing area at Minnesota Zoo

Water is provided in two pools, one of which is located near the front of the exhibit within view of the platform and the other near the back, out of view. In addition to the main viewing area, the lemurs can be seen from one side of the enclosure. There are several species of native Malagasy plants growing in the enclosure: Travelers palm (*Ravenala madagascariensis*), Madagascar Dragon Tree

(*Dracaena marginata*), Elephant Ear (*Alocasia sp.*), *Schefflera myriantha*, Bamboo (*Oxytenanthera sp.*), and Areca Palm (*Dyopsis lutescens*). Although these plants are not intended as food items, the lemurs were observed to forage on the Areca Palm. The lemurs are on exhibit during operational hours of the zoo, which was 0900 – 1600 hours throughout the study. In the evening, they are shifted to a holding area consisting of two connected cages that contain enrichment items such as balls, hammocks, and puzzle feeders. At 0700 hours, they are provided 310g to 435g of mixed fruits and vegetables (apple, papaya, banana, cooked yams and carrots, and green beans) in a bowl. In the evening they receive 300g of Purina Monkey Chow brand biscuit drizzled with fruit juice, 200g of collard greens, and 125g of grapes divided among three bowls.

3.2 Data Collection

Ethogram

An ethogram was developed (see Appendix A) and refined during a short pilot study conducted June - July 2010 at Blank Park Zoo. The ethogram was created to incorporate the methodology from several studies conducted on wild, captive free ranging, and zoo housed ring-tailed lemur troops [Dishman et al. 2009; Ellwanger 2002; Jolly 1966a; Keith-Lucas et al. 1999; Law 2008]. Each behavior was assigned to an active or an inactive category based on the amount of perceived energy expenditure and categorization used by studies mentioned previously. Activity included foraging, locomotion (walking, climbing), aggressive behaviors (biting, chasing, cuffing), and grooming. Inactive behaviors were resting and sunning.

Vocalizations and out of sight observations were not given active/inactive assignments.

Data collection

Data were collected during operational hours at each zoo between September and November 2010. During this time, data were collected on alternate weeks at each zoo. All observations were made during operational hours, when the zoo was open to visitors, beginning at the hour of zoo opening and ending at the hour of zoo closing. Observations were made throughout the day in 10-minute continuous focal subject sampling periods [Altmann 1974]. Total observation times are noted in Table 3.3. The time of day and order of sampling was randomized using Microsoft Excel random number generator [Mitchell and Hosey 2005]. Each day was divided into three time blocks (morning, noon, and evening), and every attempt was made to ensure that observations of each animal were spread throughout the time blocks over the course of the study. The duration of each behavioral state of interest (Appendix A) was recorded to the nearest second using a digital watch. States, as defined by Martin and Bateson [1993] are behavioral patterns that are measured by their (relatively long) duration, while events are defined as behaviors that are measured by frequency. The time and individuals involved in behavioral events were noted to the nearest second. Whenever possible *ad libitum* sampling [Altmann 1974] was employed to record behaviors of interest on non-focal animals. *Ad libitum* sampling most often occurred when two nonfocal individuals were engaged in agonistic behaviors, which were more easily observed in nonfocals than subtle

behaviors such as grooming. In addition to on-site observation, at least three hours of video were recorded at each location. This technique facilitated individual identification of animals and the creation of what has been referred to as a behavior encyclopedia [Tesch et al. 1998].

Minnesota Zoo	Hours	Blank Park Zoo	Hours
AM	9.05	LB	8.34
EL	9.35	OM	8.44
LI	9.67	RF	8.22
OL	9.57	SF	8.69
UR	10.00		
TOTAL	47.63	TOTAL	33.69

Table 3.3 Total observation times in hours for each individual

Visitors, enclosure size, and other variables

The number of visitors in the observation area was recorded at the end of every 10-minute behavioral sampling bout. If a count was not taken between 10-minute sessions, it was obtained at the next available opportunity. Previous studies on visitor effects have shown that the age/sex class of visitors does not alter captive animal behavior [Cottle et al. 2009]. Therefore, demographic data were not collected on visitors.

The type of environmental enrichment available to the lemurs was recorded when present. At Blank Park Zoo, the keepers provide feeding enrichment when

time allows. Enrichment observed over the course of the study was all food based, and included improvised puzzle feeders, Kong™ toys stuffed with peanut butter, and food scattered throughout the exhibit (Figure 3.2). Minnesota zoo provides no enrichment to the lemurs while on exhibit. Climatic conditions including temperature, cloud cover, and precipitation were determined using data obtained from the Weather Channel mobile phone application. This application used GPS to provide weather information for my location within each city. Weather data was taken *ad libitum*, typically during period of animal inactivity, scheduled observer breaks, or when weather conditions changed (noticeable increase or decrease in temperatures, beginning or end of rain events, rapidly changing cloud cover, etc.).

3.3 Data Analysis

I entered all data into Microsoft Excel and summarized them using Excel's Pivot table function. Pivot tables allowed the data to be summarized in a variety of ways. For each zoo, the pivot table summarized information across all animals and for each individual. The reports provided a total number of observed hours for each animal, for each behavior and the amount of the each animal engaged in a behavior as well as the percent of the total observed time. For example, Little Boy was observed for a total of 8.35 hours, 24.77% of the total observation time at Blank Park Zoo. He was observed to sun 3.78% or 1.28 hours of his total observed time, while all the lemurs together sunned for 2.61 or 7.74% of the total observation time. Statistical analyses were performed using Vassar Stats (<http://faculty.vassar.edu/lowry/VassarStats.html>), a free statistical computation

website which is both user friendly (does not require the use of scripts) and performed the necessary nonparametric analyses. Nonparametric statistics (Mann-Whitney U, Kruskal-Wallis, and Chi-squared tests) were used because the data were not normally distributed and could not be transformed. Testing for normalcy also indicated that there were no outliers in the population for any of the tested behaviors. The available data on wild lemur populations consists of summary statistics presented as percentages, and therefore statistical analyses do not produce meaningful results. For example, observed rates per hour of a behavior differ in significance if rates are calculated as seconds, minutes, or hours. Without first hand knowledge of the method of collection, this discrepancy does promote confidence in the results of the statistical analyses. Therefore, all data from the literature were compared to data collected in this project qualitatively.

CHAPTER 4: RESULTS

4.1 Comparison to wild population

The results suggest that the captive population is engaging in most species-specific behaviors. However, the level of expression of these behaviors is dependent on several components in the captive environment, such as access to foraging opportunities and natural light. The lemurs in this study differed from wild and provisioned free-ranging populations in several aspects, including levels of activity, amount of time sunning, and frequency of agonistic interactions. The lemurs at both zoos spent more time resting or grooming (inactive) than the wild, free ranging populations. BPZ lemurs spent only slightly less time resting and grooming than the semi-free ranging population at St. Catherine's Island (Figure 4.1). Overall inactivity includes both resting and sunning behaviors. The lemurs at the Minnesota Zoo sunned infrequently (0.36%) compared to both the Blank Park Zoo troop (7.74%) and rates documented in the literature for unprovisioned wild lemurs (5%) [Rasamimanana et al. 2006]

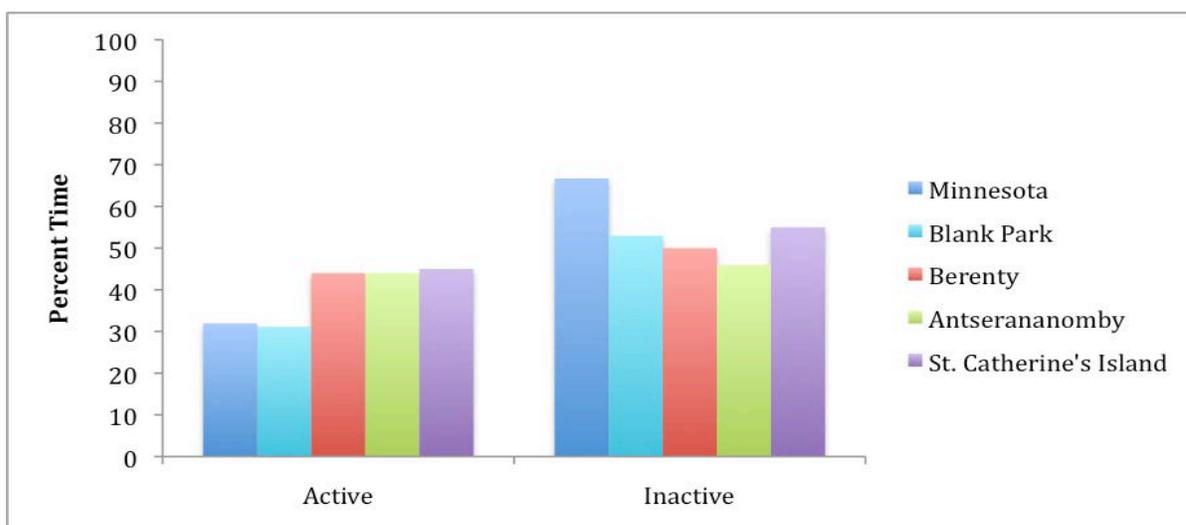


Figure 4.1. Levels of activity for captive, wild, and free-ranging ring-tailed lemur populations (does not include behavior categorized as “other”).

Jolly (1966) reported an average of 7.4 agonistic interactions per hour for wild lemurs at Berenty Reserve, Madagascar during a period that included the mating season. Both captive populations displayed lower rates of aggression than wild lemurs at Berenty (Minnesota = 0.80/hour, Blank Park = 0.78/hour), but differed regarding encounters between related or unrelated individuals, which will be discussed in more detail in section 4.5.

The total percentage of time observed engaged in behavioral categories was established for each individual at each zoo. Figure 4.2 displays the percentage of time for individuals observed at Minnesota Zoo, and Figure 4.3 provides the same information for the individuals at Blank Park Zoo. It is clear that the individuals at both locations engage in similar behaviors, although behaviors categorized as events (vocalizations, cuffing, and biting) are not included here. The rates of event

behaviors and the variability of the behaviors shown in the figures are discussed in the following sections.



Figure 4.2 Percentage of time spent in all behaviors by lemurs at the Blank Park Zoo.

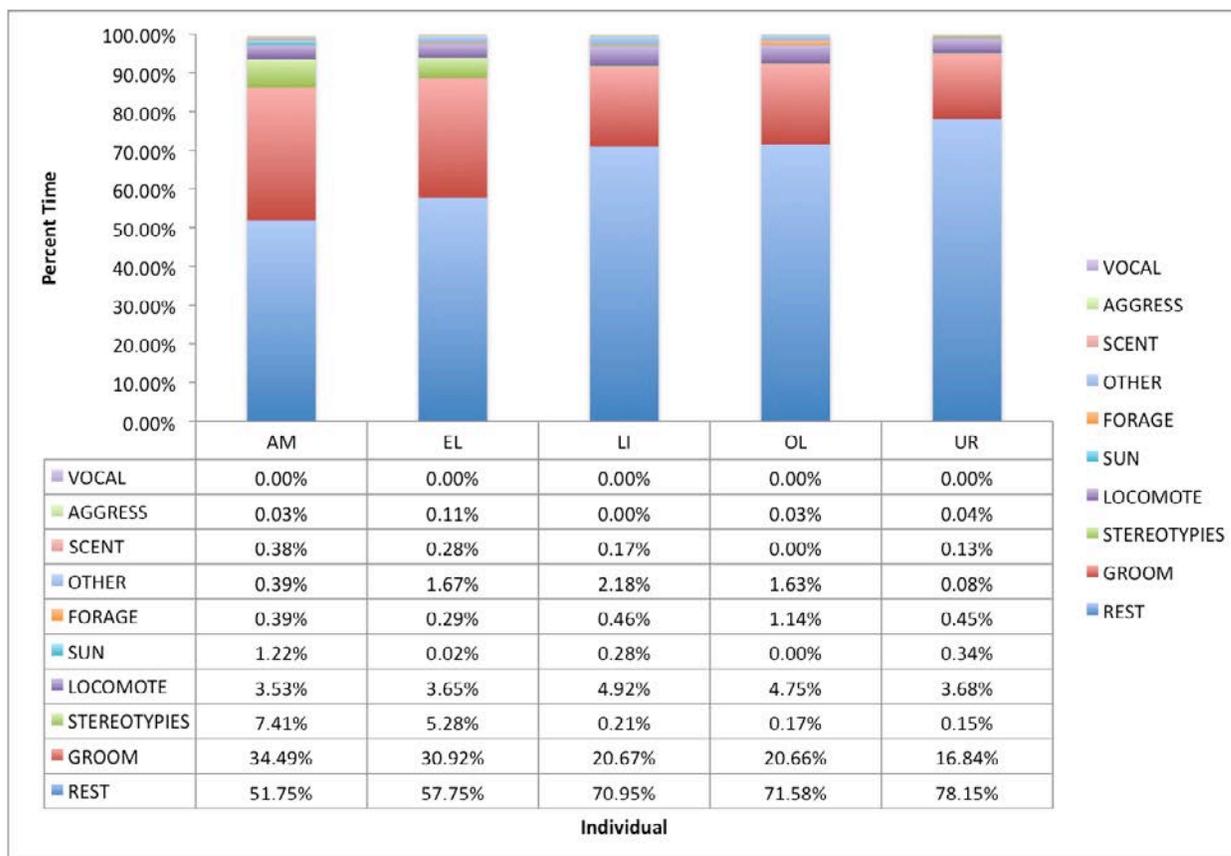


Figure 4.3, Percentage of time spent in all behaviors at the Minnesota Zoo

4.2 Zoos: Active vs. Inactive

Behaviors were divided into active or inactive categories (see Appendix A). There was a significant difference between the two zoo populations in activity levels. Minnesota lemurs (housed indoors) were inactive 66.71% of the time, while BPZ lemurs (housed outdoors) were inactive 52.95% of the time (Figure 4.4). To test for statistical differences, a Mann-Whitney U test was performed the amount of time for each observed period of activity versus those of inactivity. This approach was chosen because I wanted to determine if there was a difference in the time that each troop_of lemurs was active or inactive, rather than assess differences between

individuals. While testing for normalcy in the distribution of the sample, no outliers were detected; therefore pooling together all individuals for analysis is warranted.

The results of the Mann-Whitney U showed that the lemurs at MNZ did not differ significantly regarding levels of inactivity compared to lemurs at BPZ ($U_a=3$, $U_b=17$, $U_{critical}=1$, $p=0.41$, $n_a=5$, $n_b=4$,) (Figure 4.4). There was also no significant difference in levels of activity ($U_a=14$, $U_b=6$, $U_{critical}=1$, $p=0.11$, $n_a=5$, $n_b=4$). The Blank Park Zoo lemurs were out of sight more often than the Minnesota lemurs because they had access to an indoor facility during inclement weather, which contributed to a high percentage of time with no behavioral assignment at Blank Park Zoo (15.93%) versus Minnesota Zoo (1.19%)

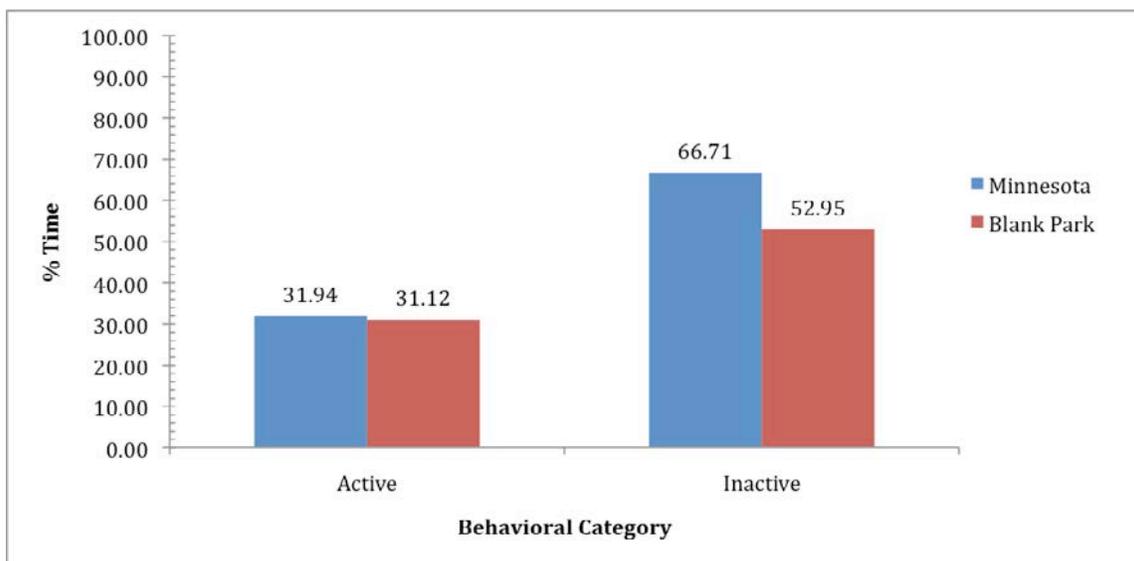


Figure 4.4 Percent of time active or inactive in the captive populations

4.3 Sunning

Wild ring-tailed lemurs have been reported to spend approximately 5% of their time sunning [Rasamimanana et al. 2006]. At both zoos, lemurs were seen to engage in sunning behavior (Figure 1.1), although only the lemurs at BPZ spent an

equal or greater amount of time sunning as wild lemurs (7.74%). Both exhibits provided the opportunity to sun, either via direct access while outdoors or through the glass roof of the Tropics House at Minnesota Zoo. As demonstrated by a Mann-Whitney U test, the lemurs at BPZ spent significantly more of their time sunning (7.74%) than lemurs at Minnesota (0.36%) ($U_a=20$, $U_b=0$, $U_{critical}=1$, $p=0.01$, $n_a=5, n_b=4$).

4.4 Stereotypical and Abnormal Behaviors

The only stereotypical behavior observed at either zoo was overgrooming. Indicators that distinguish overgrooming from normal grooming included areas of missing or thinning fur on the haunches, sides, or legs. Overgrooming due to being groomed by another individual was indicated by bald patches on areas that cannot be reached by the individual, such as the top of the head or between the shoulders. Adult female Rafiki was the only lemur at BPZ to display any abnormal behavior. Instead of licking or grooming one area for extended periods of time, as seen in most overgrooming, as part of a longer grooming bout she would place her hand in her mouth and gently chew on it (Figure 4.5). Although I did not note which hand she chewed on more frequently, all of the available video of her chewing behavior shows her left hand in her mouth. This activity comprised 1.95% of her total observation time. No other lemur was seen to engage in this behavior, and there is no record of it in this form in the literature on ring-tailed lemurs. It was not categorized as self-injurious because there were no indication of fur or skin abrasions, and she was never seen to break the skin with her teeth, The hand chewing could be categorized

as a stereotypy because it did not vary in presentation and lacked any obvious goal or function [Garner 2005]. None of the keepers at BPZ had seen this behavior prior to the study, which I believe is because Rafiki will give contact calls when a keeper approaches the exhibit, thus interrupting the behavior if it is in process. Showing video to the keepers confirmed that they had not seen it in her or other lemurs. There was no mention from the keepers that she had sustained any injuries to her hand because of the behavior.

In contrast to the lemurs at Blank Park Zoo, all the lemurs at Minnesota Zoo were seen overgrooming. For all lemurs, overgrooming composed 2.55% of the total observed time. Individual time spent overgrooming varied greatly in the troop, ranging from 7.41% to 0.15% of individual time, but the amount of time did not differ significantly between individuals (Kruskal-Wallis, $H=5.435$, $df=4$, $p=0.245$) (Table 4.1).



Figure 4.5 Rafiki chewing on her hand

Individual (MN)	% time overgroom	Individual (BPZ)_	% time overgroom
AM	7.41	RF	1.95
EL	5.28	OM	0
LI	0.21	LB	0
OL	0.17	SF	0
UR	0.15		

Table 4.1: Percent of time spent overgrooming at MN versus BPZ

4.5 Agonistic Behaviors

The types of agonism that were observed were biting (BI), cuffing (CU), and chasing (CH). In the context of this study, biting was the least aggressive behavior, used to displace another individual or end unwanted grooming. No bites were seen to break skin or draw blood. Biting was the first in a sequence of behavior, and was always preceded by cuffing or chasing. There were little or no vocalizations associated with biting. Cuffing was frequently accompanied by a squealing vocalization, in what Jolly (1966) called spats. The most intense behavior was chasing, which also involved vocalizations. Chasing was never observed to be the first in a sequence of aggressive behaviors. It typically followed a brief exchange of cuffs. Play chasing was differentiated from aggressive chasing by accompanying vocalizations (squealing or spat-meow) [Jolly 1966].

The group at Blank Park Zoo was composed primarily of males (three of four adults), while the group at Minnesota was primarily females (four of five adults), which may have implications for agonistic behavior. Behavior classified as agonistic included cuff (CU), chase (CH), and bite (BI), and all of these behaviors were

observed at both zoos. At MNZ, agonistic behaviors that were directed at or received from the red ruffed lemurs were not included in the analysis as they are not relevant to the rate of aggression between conspecifics. It is worth mentioning encounters with the red ruffed lemurs as they help to form a more cohesive picture of the overall wellbeing of the lemurs. During the observational period, most of the agonistic behaviors involving both species were directed at the red ruffed lemurs (as opposed to being initiated by the red ruffed lemurs and directed toward the ring-tails). The ring-tailed lemurs chased the red ruffed lemurs in seven out of 14 events, primarily displacing them from the central perching tree. The ring-tails were noted to move from a resting spot due to encroachment from the red ruffed lemurs four times and were lunged at, cuffed or chased by the red ruffed lemurs five times. Overall, the rates of direct encounters were relatively low, but there were clear indications that proximity to the red ruffed lemurs caused anxiety in the ring-tailed lemurs. See the discussion for further information on the interactions between the two species.

Each zoo population exhibited low levels of agonism compared to wild ring-tailed lemurs. Jolly (1966) reported 7.4 agonistic interactions per hour in wild lemurs at Berenty, Madagascar. Both captive populations exhibited less than one agonistic interaction per hour (MNZ = 0.95 per hour, BPZ=0.7716 per hour). To determine if the frequency of agonistic behavior differed significantly between the two zoos, a Mann-Whitney U test was performed, using the rate of aggression per hour for each individual (number of aggressive encounters/total observation time for the individual). The results indicated that there is no statistical difference in frequency of aggression between the two zoos ($U_a=7$, $U_b=13$, $U_{critical}=1$, $p=0.56$, $n_a=5$, $n_b=4$).

The rates of aggression between kin and non-kin were also analyzed for each zoo population using a Chi square test of association. The results indicate that there is an association between kin status and rates of aggression ($df=1$, $N = 60$, $Yates=14.27$, $p=0.001$).

4.6 Visitors

Visitor counts were taken every 10 minutes to determine the effect of visitor numbers on the expression of stereotypical or abnormal behaviors in the lemurs. Table 4.2 summarizes the totals and averages for each zoo. BPZ and MNZ had 1.21 and 3.62 visitors on average for each 10-minute count and an hourly average of 8.9 and 22.4, respectively. The percent of time engaged in stereotypical behavior per day was plotted against the average number of visitors per day, and a second order polynomial relationship was found ($R^2 = 0.13025$) (Figure 4.6). This suggests that higher and lower numbers of visitors result in fewer stereotypical behaviors than a medium number of visitors. There were several data points that appeared to be outliers, so the analysis was run with and without the highest value (13) ($R^2 = 0.10131$) and the lowest values (0) ($R^2 = 0.10077$). In all cases, a second order polynomial was the best fit for the data, although the low R^2 values indicated a weak correlation (Fig 4.6). A linear relationship was a poor fit; therefore progressive curvilinear lines were applied until a best fit line was formed that did not exceed a quadratic relationship [Martin and Bateson 1993]. The highest value day occurred at Minnesota Zoo on October 22, 2010, when all the public schools in the state had the day off from school, and it therefore does not necessarily reflect the normal flow of

people through the zoo. Additionally, there were two days of observation at Blank Park Zoo when the lemur exhibit was closed to the public due to the annual Night Eyes event.

	Blank Park Zoo	Minnesota Zoo
Average per day	43	156
Average per each 10-minute count	1.21	3.62
Average per hour	8.9	22.4
Total for study period	301	1098

Table 4.2 Visitor counts

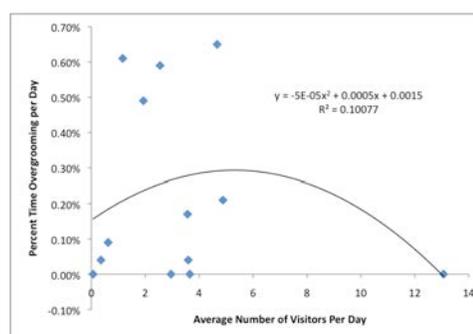
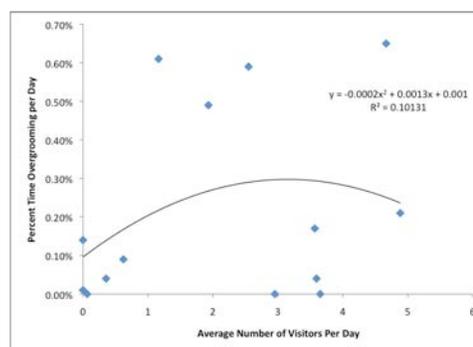
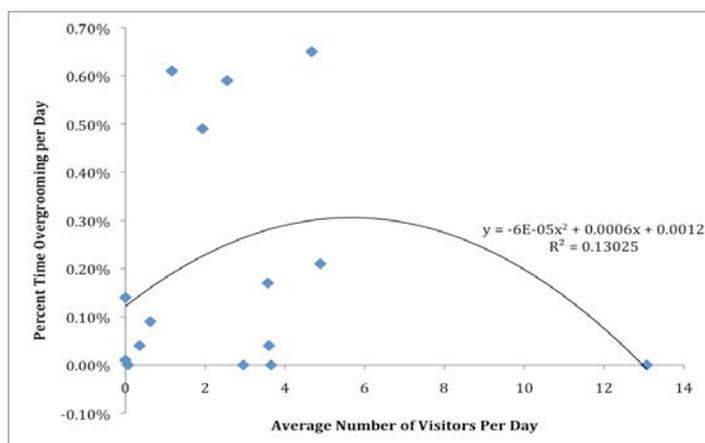


Figure 4.6 Above: Percent time overgrooming as a function of average number of visitors per day. A second order polynomial relationship exists between the two, suggesting that high and low numbers of visitors result in lower stereotypical behaviors. Right top: same analysis without highest number (13). Right bottom: same analysis without lowest numbers (0)

CHAPTER 5: WHY STUDY SPECIES-SPECIFIC BEHAVIORS OF CAPTIVE ANIMALS?

Although there have been no confirmed primate extinctions in the last 300 years, the IUCN Red List identifies 37 critically endangered, 86 endangered and 78 vulnerable primate species, putting 48% of all primate species at risk [IUCN 2010]. This has prompted the IUCN Primate Specialist Group to regularly publish a list of the top 25 endangered primates. The main causes of primate population decline are habitat destruction, hunting and illegal pet trade [Mittermeier et al. 2009]. Primates are at particular risk for losing behaviors in captivity as watching and interacting with other individuals are their primary modes of learning [Hosey 2005]. The complex social networks that most primates navigate through touch, body language, and vocalizations are essential to survival in the wild and are not encouraged in captivity [Van Hooff 1986]. Captive males do not have to establish dominance for mate or food access with the same urgency as wild males. Food is ample, and mates are chosen for them based on criteria that maintain optimal genetic diversity in the captive population. Individuals that are unsuccessful in captivity (i.e. hostile or aggressive toward humans) are not bred, although they may be best suited to survival in the wild [Ryder 1995]. These captive populations are the genetic and behavioral stock that will one day be the foundation for reintroduced populations. Reintroduction programs are a difficult undertaking and require several years of preparation, post-release monitoring and support, and many dollars for funding. Successful programs, such as the Golden Lion Tamarin (*Leontopithecus rosalia*) project, have had to undergo extensive training or re-training of animals, including

predator avoidance and locomotion behaviors, adding to an already costly and time-consuming undertaking [Dietz et al. 1987; Kleiman and Rylands 2002]. Maintaining these behaviors in captivity decreases the amount of time and money spent on training and potentially increases the chances of survival in the wild. The results of this study will help to direct efforts for behavior maintenance by determining how the frequency or expression of behaviors is affected by captivity.

5.1 Agonistic Behaviors

My results do not support the hypothesis that lemurs housed in abnormal social groupings (primarily male or primarily female) differ in their rates of aggressive encounters. The data do indicate a trend toward non-kin engaging in aggressive behavior more with each other than they will with related individuals. Similar to the results of my study, lower frequency of kin as targets of aggression in captivity has been seen at Duke University Primate Center [Pereira 2006]. Pereria [2006] found that matrilineal sisters did not aggressively target each other often, and that mother and daughters never targeted each other. At the Minnesota Zoo, 38 agonistic interactions were observed. Three were between Lisa and Elizabeth, matrilineal sisters. Lisa and Elizabeth each targeted their mother (Ursula) only once, resulting in only 13% of aggressive encounters occurring between related females. In contrast, the unrelated female Amanda, believed by staff at the zoo to be the dominant female, targeted others 37% of the time. Lisa, Elizabeth and Oliver each received four or five aggressive acts. Ursula, at 20 years old, was spared, only being cuffed by Amanda once. Oliver (unrelated male) was the most frequently abused (32%),

followed by Lisa and Elizabeth (sisters) (21%), Amanda (18%), and Ursula (mother of Lisa and Elizabeth) (8%). It is not possible in the context of this study to determine if Amanda's increased rates of aggression are a result of not being related or due to dominance. However, given the lower rates of aggression between the sisters, research on different groups of captive lemurs is warranted.

At Blank Park Zoo, Little Boy, the youngest male, initiated half of agonistic interactions (total observed = 26; nonkin =10, kin=16). Of those, 69% were directed at his brother, Scarface (Little Boy administered the blow that created the scar for which Scarface is named prior to the start of observations). Little Boy was never observed to direct any aggression towards Rafiki, although 30% (total observed=10) of her agonistic interactions were directed at him. The primary target of Rafiki's aggression was Old Man (60%). She was never observed to chase another lemur, but she did utilize a cuff as a warning signal to end unwanted grooming, or to displace another individual and reinsert herself in the vacated position. The latter behavior was observed most often when individuals were resting in contact with each other (Figure 5.1).



Figure 5.1: Lemurs resting in contact at Minnesota Zoo

5.2 Inactivity

Most of the lemurs' observed time was spent in an inactive state, which involved sitting, resting, or sunning. Sitting behavior occurred with the head up, allowing the individual to observe their surroundings. Resting occurred with the head placed down against the chest. No attempt was made to distinguish if the individual rested with their eyes opened or closed. Lemurs in the wild spend 50-55% of their time inactive. Jolly observed that a typical lemur troop wakes before dawn and spends the hours after dawn until 0830 hours moving, sunning, or feeding. The troop moves to a feeding location by 1000 hours and feeds for about two hours. At noon, the troop may rest for up to four hours, followed by another feeding period and movement to sleeping trees [Jolly 1966a]. This pattern was repeated in both zoos, with most activity occurring immediately after release into the exhibit, and then tapering off into inactivity throughout the day. The lemurs would then become active

again in the period directly preceding the opening of the night enclosures. The lemurs in this study tended toward being more inactive than wild lemurs, spending a majority of their time resting or grooming.

5.3 Sunning

Lemurs in this study housed indoors sunned less than those housed outdoors, despite having exposure to natural light through a glass roof. Sunning is a species-typical behavior used by ring-tailed lemurs for thermoregulatory purposes [Rasamimanana et al. 2006] and is found in all wild populations. Therefore, it is a good measure of the ability of the captive environment to elicit natural behaviors. At Blank Park Zoo sunning occurred throughout the enclosure, and lemurs moved locations as sunny spots changed throughout the day. BPZ lemurs spent 7.74% of their time sunning, higher than predicted. The increased time sunning may be a result of being outdoors and exposure to fluctuating temperatures. However, unlike wild lemurs, which can move freely between locations and generate body heat in the process, the captive lemurs are limited in their ability to move and thus generate sufficient heat. Therefore, the lemurs may have increased sunning frequencies in order to maintain a comfortable body temperature. The enclosure provided ample sun and shade, allowing the lemurs to move freely between warmer and cooler areas (Figure 5.2). Individuals were observed to fall asleep while sunning and lose their balance, resulting in what appeared to be a slightly drunk, meditating lemur. All lemurs at BPZ spent time in the sun, but Old Man and Rafiki did not adopt the traditional sunning position often. Perhaps due to his advanced age or normal

individual variation, Old Man sat with his ventral surface toward the sun, but slumped instead of sitting upright. Rafiki's posture was similar to Old Man's, but her lack of upright stance may have been because of her large breasts rather than old age. Her history as a pet may also have influenced her sunning position. It is possible that she had no experience with sunning prior to zoo placement. Toward the end of the study period, temperatures fell in to the 3° to 5° C range, and the lemurs at BPZ had access to their indoor enclosure. However, they were still observed to sun while outdoors during colder days, underscoring the thermoregulatory function of the behavior. It is unknown if the lemurs at BPZ attempt to sun while indoors during the winter months, but anecdotal evidence from the staff indicates that they will sun during warmer winter days when they are provided with outdoor access.

In contrast to the BPZ lemurs, the Minnesota Zoo lemurs were only observed to sun 0.36% of the observational period. The building in which the exhibit is housed has a glass roof, which provides ample natural light, but little opportunity for direct sun. During the study period, the only time direct sunlight entered the enclosure was during a brief period in the morning, and only on days when there was little or no cloud cover. Given that this study was conducted during late fall/early winter, it is possible that more direct sunlight may enter the exhibit during summer months and stimulate more sunning behavior. It is possible that the primary reason for lack of sunning was the location of sun in the exhibit. The lemurs at Minnesota Zoo are housed in a multi-species enclosure with red ruffed lemurs. Agonistic interactions, primarily in the form of chasing or cuffing, were observed between the two lemur species. Staff at the zoo informed me that the red ruffed lemurs typically occupy the

outer and upper edges of the enclosure, which consists of a rocky wall, while the ring-tailed lemurs remained on the center tree structure. A majority of direct sunlight fell on the upper rocky areas, and although the ring-tails were observed to sun on those areas, they may have limited access due to the territorial nature of the red-ruffed lemurs.

Sunning is a behavior that lemurs use to lower the energy associated with thermogenesis, and although captive lemurs do not have the same energy stresses as wild lemurs, it is still an important indicator of the ability of the captive environment to initiate species typical behaviors. In this manner, the enclosure at MNZ is lacking. Not all of the individuals at Minnesota sunned during the study period. Elizabeth and Oliver were not seen to sun at all. Amanda, apparently the dominant female, controlled most of the available sunlight, displacing Lisa and Ursula when necessary. There is no reason to assume that the lemurs at Minnesota do not know how to sun, as all the females come from St. Catherine's Island, where sunning is observed as a part of daily behavior patterns [Keith-Lucas et al. 1999]. The lack of sunning is more likely a result of either a thermocontrolled environment or lack of appropriate sunning locations or opportunity. A small heat lamp is positioned just above the heads of the viewing public (Figure 5.4), presumably to warm the enclosure and to draw the lemurs closer to the viewing public. During the course of the study, the red ruffed lemurs used the mesh netting to position themselves ventral side down against the lamp, much to the delight of zoo visitors. (Although that delight was short-lived when visitors realized that urinating often followed). The ring-tailed lemurs never used the heat lamp in the same manner as

the red ruffed lemurs, but they may have used the body heat of conspecifics to aid in thermoregulation (personal observation).

Although sunning is frequently referred to as a species-typical behavior, there is a lack of information on the percent of time lemurs spend engaged in sunning behavior. Rasamimanana *et al.* [2006] reported a value of approximately 5% in the wild. Comparatively, lemurs at BPZ sunned considerably more, while those at Minnesota sunned considerably less. The results of this study suggest that the difference in sunning behavior is more likely a result of the type of housing, rather than the captive condition.

5.4 Stereotypical Behaviors

The results of my study support both hypotheses regarding stereotypical behaviors: that lemurs housed indoors will spend more time engaged in stereotypies, as will those that have more visitors to their enclosures. The only lemur at Blank Park Zoo seen to engage in any stereotypical behavior was Rafiki, an individual that was hand-reared by humans as a pet. Although it is unconfirmed, she may have been a companion animal for a long-distance truck driver. Her hand chewing behavior may have developed as a way to clean and/or remove the last remnants greasy, salty or other atypical foods from her fur. In addition to her hand chewing, Rafiki vocalized (typically a meow) at familiar people, primarily zookeepers, and in response to her name. Former pets and hand-reared individuals are becoming increasingly rare in the zoo population. Current population management practices emphasize the need to maintain the genetic diversity of captive populations, and thus individuals with

unknown pedigrees and those that have been hand reared are excluded from breeding programs [Villiers 2009]. At Minnesota Zoo, all the lemurs were parent-reared, and all the females had been part of a semi-captive free ranging colony prior to being transferred to traditional zoo environments. All individuals were observed to engage in stereotypical overgrooming, although to varying degrees.

Captive prosimians are known to exhibit a variety of stereotypies, including pacing, somersaulting, overgrooming, and self-injurious behavior, with a majority of these behaviors occurring in populations housed indoors and while off exhibit [Tarou et al. 2005]. Although one individual at Blank Park Zoo engaged in what was classified as overgrooming, her behavior is not typical. Lemurs do not use their hands to manipulate objects like other primates. Object manipulation is typically achieved by pulling the object toward the face and using the mouth to explore or maneuver an object [Jolly 1966a]. Throughout the course of this study, lemurs at both zoos were observed grasping the branches of vegetation with their hands and pulling it to their mouth rather than pulling leaves from the branch and placing those in the mouth. Provisioned food was grasped with the hands and placed in the mouth, but the lemurs were never seen to pull apart food items prior to ingestion. Therefore, it is unlikely that her hand chewing behavior has origins in normal foraging techniques.

Stereotypies often emerge as a way for captive individuals to deal with stress and boredom, elements that are common in captive environments [Carlstead 1996]. Individuals that are unable to perform normal behaviors or normal rates of behavior will channel those energies into repetitive behavior patterns that serve no goal or

function other than to alleviate stress. Well documented in both carnivores [Carlstead 1996] and anthropoid primates [Hosey 2005], there is very little published information on the effects of captivity on prosimian primates, and even less on *Lemur* species [Tarou et al. 2005]. For captive prosimians, *Lemur* species are significantly less likely to exhibit stereotypes than *Varecia*, which the authors suggest is a result of the more arboreal and territorial nature of the latter [Tarou et al. 2005]. The authors also found that individuals that were never provided with enrichment items were less likely to have stereotypies than did individuals that received enrichment items on a regular basis, and that exhibit type (indoor/outdoor) did not predict the presence of these behaviors. This conflicts with my observations. Minnesota Zoo adheres to an “all-natural” exhibit design and provides no enrichment to the lemurs while on exhibit. The indoor enclosure, lack of foraging opportunity while on exhibit, and stress from being housed with the more aggressive red ruffed lemurs all stand out as elements that would trigger overgrooming.

In contrast to the Minnesota Zoo lemurs, those at Blank Park Zoo are housed outdoors, receive regular enrichment, have many opportunities to forage on both provisioned food items and vegetation, and only have to deal with the occasional bird, thieving chipmunk or noisy squirrel. These results should not be extrapolated to the winter months when the BPZ lemurs are kept exclusively indoors. When questioned about winter behavior, zoo staff members were unsure if there were any abnormal behaviors or any abnormal expressions of behaviors. The possibility for quantifying overwinter behavior at Blank Park Zoo exists, although observations would require the use of video cameras, as the lemurs are not accustomed to being

observed indoors, and the building is too small for observers to maintain a safe distance from the lemurs, as dictated by zoo protocol.

5.5 Recommendations

There are several alterations to the habitat and husbandry practices at MNZ that I suggest could decrease the level of overgrooming. The most significant difference between the two zoos in terms of specific behavior was the time spent foraging. The lemurs at BPZ had many opportunities to forage throughout the day on provisioned food items and on growing vegetation. At MNZ, the lemurs were seen to chew on the leaves of the Areca Palm within the enclosure. Zoo staff reported that the plant was not intended as a food item, as it was time consuming and costly to provide continued replacement for damaged plants. Kevin Willis, the director of Bioprograms at MNZ informed me at the beginning of my observational period that the zoo strives to make all exhibits naturalistic – meaning that no non-natural items, including enrichment and provisioned food, are permitted in the enclosures.

Although it is valuable for the zoo going public to see lemurs surrounded by the native Malagasy vegetation, it would be more beneficial to the lemurs and the public to see them engaged in natural activities that are more indicative of a wild state.

Simulating natural behaviors involves providing the animal with an environment that mimics the wild habitat to encourage behavior expression while stimulation relies on environment enrichment to evoke the behavior regardless of the enclosure [Fábregas *et al.* 2011, Grandia *et al.* 2001]. Visitors are more likely to stay engaged with an active animal longer than an inactive one [Margulis *et al.* 2003] and given

that ring-tailed lemurs are already inactive for over half of the day, encouraging any increase in activity is beneficial for all species involved. Throughout the course of the study, I heard visitors refer to sleeping lemurs as both “boring” and “lazy” and were prompted by active lemurs to ask questions, read signage, and engage their children in active observation.

Feeding on exhibit at MNZ is confounding by the presence of the red ruffed lemurs, as they present a form of feeding competition. Red ruffed lemurs are the largest lemur species, and are currently restricted to the Masoala Peninsula in Northern Madagascar. It is contrary to the zoo’s naturalistic enclosure approach to house the red ruffed lemurs with the ring-tailed lemurs as their habitats do not overlap in the wild. The more aggressive nature of the red ruffed lemurs is at odds with the more playful, relaxed attitudes of the ring-tails, although is not unheard of to house the two species together. At one point, BPZ attempted to keep ring-tailed and red ruffed lemurs together in the current ring-tailed lemur exhibit. The choice was made to remove the red ruffed lemurs after continued aggressive encounters initiated by larger lemurs that included chasing and biting. At MNZ, some of the indentifying features of individuals (missing parts of fingers) were a result of encounters with the red ruffed lemurs. Removing the red ruffed lemurs from the exhibit will not only facilitate incorporating on exhibit feeding but could likely decrease stress caused from aggressive encounters and may increase sunning behavior, as the lemurs will have full access to the entirety of the exhibit space.

Note: Video

Video was taken throughout the study at both sights, both handheld and set up on a tripod. The video provided useful information for my analyses and was helpful when asking keepers about specific behaviors (Rafiki's hand chewing behavior). Video segments were randomly chosen and checked against onsite data to determine if behavioral classification and individual identification was consistent. Video footage will be made available to the zoos and to other researchers in the hopes that it will help to maintain a standard ethogram for studies of this kind. Although I found the video to be a useful tool, the camera set up would need to be improved if it is to be used to record the behaviors of all lemurs in the exhibit for an entire day. The camera itself will need to have a wide angle lens that can capture the entire enclosure with minimal out of sight areas, and high enough recording resolution to allow zooming in on individuals during coding. Using multiple cameras to record simultaneously is one way to record all areas. Access to outlets is limited or nonexistent in the two locations used for this study, and most moderately priced digital camcorder batteries can record at high resolution for about two hours, necessitating several batteries for a full day of observation. Although a multi-camera set up is expensive to purchase, and coding video takes longer than onsite observation, this approach can be a valuable tool for constructing true activity budgets. Time stamps on the video can increase the precision of data collected on the duration of behaviors. Due to the confined space in a captive environment, what one lemur is doing at any given moment is influenced by several factors including other individuals, visitors present, temperature, the activity of zoo staff, and activity

of animals in nearby enclosures. An observer using a camera set up to record behaviors would be able to incorporate more of these factors into observation than one without, thus capturing a more accurate picture of what elements of captivity alter behavior.

5.6 Future Directions

Zoos are a particularly important component of the reintroduction process for animal species, as they are “pre-adapted” to maintain populations of threatened species due to their histories of keeping, breeding and transporting animals. It is this very experience however, that leads some authors to criticize their ability to be an effective part of species conservation. It is estimated that there are 1,000,000 animals housed in zoos globally, and that most of these animals are higher order vertebrate species, such as felids and primates [WAZA 1983]. These zoos are visited by at least 600,000,000 people annually – approximately 10% of the world’s population [WAZA 1983]. Zoos are primarily viewed as a form of entertainment by the public, and zoological parks depend heavily on admission fees to fund their operations [Knowles 1977]. Therefore, zoos have made conservation decisions to maximize the financial return from breeding endangered species for exhibition [Knowles 1977]. Over time, this has led to an over-representation of certain rare species in zoos.

Despite the criticism of zoos as conservation entities, organizations such as the AZA began drafting Species Survival Plans (SSP) in 1981. These plans require the participation of AZA accredited institutions and their affiliates in the management

and conservation of selected species. There are currently more than 300 SSPs, each governed by a Master Plan that provides necessary guidelines for captive breeding, including assessing demographic information and keeping studbooks. In addition to the AZA, the World Association of Zoos and Aquariums (WAZA) supports *ex situ* conservation efforts in institutions globally as a complement to *in situ* conservation. WAZA maintains the stance that collections in individual facilities are insufficient to work as stand-alone conservation entities and works toward a collaborative global effort in the form of cooperative breeding programs. These programs take the form of regional organizations that exchange animals [WAZA 2009]. WAZA supports the AZA as well as its European, Australasian, African, and Japanese counterparts in these efforts.

The low success rate of reintroductions (ranging from 11-54%) requires a reexamination of how we maintain species in captivity [Kleiman and Beck 1994; Kleiman 1989]. Evidence suggests that reintroductions using wild stock are more successful than those use captive stock [Jule et al. 2008]. Primate reintroduction projects have only been attempted a handful of times and have often used translocated animals [Peignot et al. 2008] or individuals that have been orphaned or otherwise rehabilitated [Keith-Lucas et al. 1999 (*Lemur catta*); Tutin et al. 2001 (*Pan troglodytes*)]. Deaths of reintroduced individuals are often the result of behavioral deficiencies due to a predictable, static captive environment [McPhee 2003]. Evaluating and meeting the behavioral needs of captive animals allows managers to fulfill their roles as stewards, and provide valuable educational opportunities for zoo visitors [McPhee 2003].

The lack of multi-institutional behavioral studies conducted in zoos does not allow animal keepers, administrators, or researchers to determine how the captive condition alters the behavioral profile of a population of captive animals. Single zoo studies are essential for establishing better husbandry protocols, breeding programs, and enclosures for individual institutions but do not address the role of the zoo in conservation or loss of behavior [Carlstead 2002; Shepherdson and Carlstead 2001]. Animal welfare guidelines ensure that individuals are provided with stimulating environments, but these guidelines do not encourage behavior maintenance [AZA 2009a; AZA 2009b]. The lack of exposure to simple natural stimuli, such as wind, has prevented the initial success of reintroduction programs. In the case of the Golden Lion Tamarin (*Leontopithecus rosalia*) reintroduction the substrate that the animals experienced did not mimic the way that natural substrate moves in the wind. Upon release, several of the animals fell out the trees when the wind blew [Kleiman and Rylands 2002].

Reintroduction for captive breeding and conservation is not something that has tried and failed and will never be attempted again. The tamarin reintroduction was ultimately a huge success, far outstripping the hopes of the project managers (Beck, personal communication). Philanthropist Richard Branson recently proposed introduction ring-tailed lemurs onto an island he purchased in the British Virgin Island. He plans to import the lemurs from zoos across the globe and breed them in captivity in the hopes that these individuals will be the stock for eventual reintroduction into their native habitat [Black, 2011]. His project has been heavily criticized for not thoroughly exploring the environmental impact that the lemurs may

have on the island, but as of May 23, 2011, several lemurs have been introduced. Mr. Branson plans to keep these individuals in enclosures temporarily, rather than letting them roam freely. His proposed project is an example of the continued need to maintain captive populations that are like their wild counterparts in every possible way. The solution is not to depend on the actions of millionaire philanthropists, but to generate a body of knowledge that can guide captive managers in the care and maintenance of wild behaviors in a captive environment. To this end, I propose the following recommendations:

- 1) **Exhibits:** animals should be kept in exhibits that provide them with all possible opportunities to forage, nest, climb, crawl, or engage in any other physical activity as found in wild individuals. For the lemurs included in this study, I recommend altering the MNZ habitat so that the lemurs are able to spend more time on the ground, foraging either for provisioned food items or on vegetation provide for that purpose.
- 2) **Social groups:** Animals should be kept, whenever possible, in social groups that are most reflective of natural social systems. For ring-tailed lemurs, human assisted dispersal of males into new groups, and maintenance of 1:1 sex ratio is my primary suggestion. Keepers and collection managers will have to closely monitor newly placed males and remove them should the males experience higher than normal levels of aggression.
- 3) **Other species:** To ensure that captive animals are experiencing an environment that best represents the wild condition, animals should not be housed with species unless there is natural overlap in the ranges. Species

with overlapping range are less likely to promote stress responses (assuming we are not housing prey with predators). The red ruffed lemurs in this study were clearly a source of stress for the ring-tailed lemurs, and their presence may have contributed to rates of overgrooming.

- 4) **Feeding:** Given the amount of time that animals spend foraging, providing proper nutrition coupled with appropriate behavior can be challenging in captivity. Current welfare laws preclude the use of live prey as feeding enrichment for predators, but that should not prevent caretakers from providing the best alternative. I acknowledge that pre-formulated food items ensure that the nutritional need of the animals are being met, feeding primate biscuits on a daily basis eliminates the animal's ability to choose a varied diet. Animals in the wild have the choice to move between sources to find the most seasonally abundant (or best tasting) items. Likewise, we should provide a varied diet that, whenever possible, approximates the foods eaten in the wild, in the manner in which they are consumed in the wild. Ring-tailed lemurs forage on and off throughout the day and should be provided fruit and vegetation scattered throughout the exhibit (preferably several times throughout the day) to allow them to express this natural behavior.
- 5) **Novelty:** Underlying most of the suggestions above is the concept of novelty. The environment is constantly changing, and animals must respond to several changes at once in order to be successful. However, the captive environment is structured in such a way as to expedite the ability of keepers to attend to all the animals in their care. Varying feeding schedules and food

items, presenting new odors or other sensory stimulation, and even utilizing modular exhibit features that can be periodically changed may have substantial influence on the expression of natural behaviors.

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APPENDIX: ETHOGRAM

Behavior	Category	Abbreviation	Description
Foraging	Active	FR	When the focal animal searches for food in the enclosure either by actively moving through the enclosure or by visually searching for food items. Manipulation of food items without placing them in the mouth.
Sunning	Inactive	SN	The focal animal moves into the sunlight, torso vertical, forelimbs extended and allows solar rays to warm the body. In rare cases, this may be exhibited in the absence of sunlight.
Groom-Self	Inactive	GS	The animal uses the grooming claw or tooth comb to clean itself
Groom-Other	Inactive	GO	The animal uses the grooming claw or tooth comb to clean another individual or is cleaned by another individual
Climb	Active	CL	The animal moves about on a vertical structure, including but not limited to walking on trees, branches, locomotion on the cage itself, or leaping between substrates
Walk/Run	Active	WK	The animal locomotes terrestrially using all four limbs.
Sit	Inactive	ST	When the animal sits with head up and eyes open
Rest/Sleep	Inactive	RS	When the animal puts their head down. Eyes may be closed.
Cuff	Active	CU	The animal hits another individual using their hand in an aggressive manner. Does not include play behavior.

Behavior	Category	Abbreviation	Description
Bite	Active	BI	The animal attacks another individual using their teeth in an aggressive manner.
Vocalization Meow	---	VM	The animal opens mouth and emits a noise that sounds like "mew" or "me-ow" used as a contact call during traveling in the wild
Vocalization Bark	---	VB	The animal opens mouth and emits a yapping sound. May occur in response to a predator or neighboring troop.
Vocalization Spat	---	VS	The animal opens mouth and emits a squeak, twitter, yip, or squeal. Often occurs during aggressive encounters.
Vocalization General	---	VG	The animal emits a click, purring, or grunting sound. Occurs in a variety of contexts, such as while grooming, staring at a new object, or mobbing a predator.
Scentmark	Active	SC	The animal uses glands (such as those located under the tail, arms, wrist) to mark surfaces
Stereotypical Pace	Active	SP	The animal travels the same path repeatedly (back and forth) in succession
Stereotypical Somersault	Active	SS	The animal repeatedly turns itself head over heels. Does not occur during play or agonistic interactions
Stereotypical Overgroom	Active	SO	The animal cleans itself or another individual excessively. May result in bald patches of fur
Stereotypical Self Injurious	Active	SI	The animal uses teeth, claws, or nails to cause harm to itself, such as self-biting or chewing.
Other		OT	Other behaviors