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Examining Environmental Use by Captive Lemur catta and Varecia rubra

Rhiannon Belcher
Central Washington University, rhiannonbel71@gmail.com

EXAMINING ENVIRONMENTAL USE BY CAPTIVE

LEMUR CATTA AND *VARECIA RUBRA*

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by

Rhiannon E. Belcher

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We hereby approve the thesis of

Rhiannon E. Belcher

Candidate for the degree of Master of Science

APPROVED FOR THE GRADUATE FACULTY

______________ ________________________________
Dr. Kara Gabriel, Committee Chair

______________ ________________________________
Dr. Jessica Mayhew

______________ ________________________________
Dr. Lori K. Sheeran

______________ ________________________________
Dean of Graduate Studies

ABSTRACT

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There are over 100 named species of lemurs, of which 94% are considered threatened with extinction by the International Union for the Conservation of Nature (IUCN). They live in increasingly fragmented forests. To understand how best to protect them in their natural habitats, we can observe how they manipulate the environment and how they use objects, both natural and humanmade, around them. Understanding their behavior is a critical component of conservation, and observing behavior in a captive setting allows us to study lemur-environment relationships without disrupting what little habitat is left in Madagascar. In this study I investigated whether the object/substrate use of captive ring-tailed and red ruffed lemurs could be catalogued under several different functions at the Woodland Park Zoo, Seattle, WA. Activity budget and spatial use data I collected revealed that lemurs at the Woodland Park Zoo did not seem to spend an atypical proportion of their behaviors as inactive compared to their wild counterparts. However, neither species utilized the entirety of their enclosures, and vigilance behaviors occupied a large proportion of their activity budgets. Noise levels at this urban zoo may contribute to vigilance behavior, and mitigation techniques, such as waterfalls, may not be useful if

lemurs do not utilize all areas in their enclosures where these mitigation techniques are used. It is imperative to determine whether these mitigation techniques are truly working to reduce noise and encourage lemurs to utilize more of their enclosures so that they are exposed to less external noise from around the zoo.

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CHAPTER I

INTRODUCTION

With over 100 species having been identified, lemurs are a diverse group of primates. They are also an endangered group—94% of lemur species are considered as threatened, endangered, or critically endangered by the International Union for the Conservation of Nature (IUCN), with many of those lemur species listed as endangered or critically endangered. In addition, nearly every species of lemur is declining in numbers (Estrada et al., 2017). The risk of losing such unique primates, who still have a plethora of information about our evolutionary history left to tell us, is dangerously high.

Lemurs are commonplace in many zoos; there are somewhere between 1,800 and 2,500 lemurs living in zoos around the world, primarily ring-tailed (*Lemur catta*) and ruffed (*Varecia* spp.) lemurs (Andriaholinirina et al., 2014a). Despite this, research on the husbandry needs of captive lemurs, especially red ruffed lemurs (*Varecia rubra*), is limited. Most of the published literature on captive lemur behavior has focused on feeding enrichment devices (e.g., Britt, 1998; Dishman, Thomson, & Karnovsky, 2009). Enclosure design, however, has largely relied on research from other primates, whose needs may differ greatly from lemurs (Dye, 2017).

In the future, as conditions continue to change in Madagascar, it is likely we will need to rely further on zoos as a source of valuable genetic diversity, education to the public, and research. How lemurs interact with different substrates and objects in their enclosures, as well as their responses to potential stressors, is useful information from both a captive management and a conservation perspective. These data can inform us of the behavioral plasticity and, therefore, adaptability, of ring-tailed and ruffed lemurs, while also providing information to allow for the most effective enclosure design for captive lemurs.

CHAPTER II

LITERATURE REVIEW

Phylogeny

Lemurs are classified in the suborder of Strepsirrhini, along with lorises, galagos, and pottos. Lemurs are composed of five different families, of which ring-tailed and red ruffed lemurs are a member of Lemuridae (Dye, 2017). Strepsirrhines diverged from Haplorrhine primates between 64 and 87 million years ago, and lemurs diverged from other Strepsirrhine primates between 50 and 66 million years ago, according to molecular data (Herrera & Dávalos, 2016; Perelman et al., 2011). Endemic to the island of Madagascar, lemurs are considered the most endangered group of mammals due to habitat loss and fragmentation (Schwitzer et al., 2014). With over 100 identified species, they are a highly diverse group of primates, representing more than 20% of the world's primate species (Estrada et al., 2017).

The diversity of lemur species is remarkable, considering they exist in such a small area of the globe relative to other primate species; the landmass they inhabit represents less than 3% of the landmass containing all other primates combined (Estrada et al., 2017; Schwitzer et al., 2014). They exhibit a wide range of sizes, from mouse lemurs (*Microcebus* spp.) weighing just a few grams to the 10 kg Indri (*Indri indri*), as well as a variety of diets, including folivores, frugivores, insectivores. There are even lemurs who specialize in specific bamboo species. Lemurs provide valuable insights to the evolutionary history of primates, as they diverged earlier than other extant primate species. In addition, the singular aye-aye species (*Daubentonia madagascariensis*) is a lemur that represents approximately 30 million years of evolutionary history as the only extant species in the Daubentoniidae family (Wich & Marshall, 2016).

Conservation

McCarthy et al. (2012) estimated that adequate funding for conservation is present for less than 3% of species globally, underscoring the need for prioritization when it comes to conservation. The endemism and diversity of orchid, chameleon, and many additional plant species in Madagascar is unmatched by that of any other country, making it one of the single most important geographical areas identified for conservation (Schwitzer et al., 2013). It is the only place on the planet lemurs are found in the wild. While the endemism and evolutionary history of lemurs makes them unique, it leaves them vulnerable to habitat disturbances. Ninety-four percent of recognized lemur species are listed as threatened by the IUCN, and 97% of species are experiencing population decline (Estrada et al., 2017). Red ruffed lemurs are listed as critically endangered and ring-tailed lemurs, long considered to be the most flexible species of lemur as they are able to thrive in many different types of habitats, are listed as endangered by the IUCN (Andriaholinirina et al., 2014a; Andriaholinirina et al., 2014b).

Madagascar faces unique conservation challenges as an island, but intensifying the struggle for lemur survival is the fact that only 10% of Madagascar is suitable habitat for primates (Schwitzer et al., 2014). Furthermore, Madagascar is plagued by extreme poverty and political instability that has affected other countries' extension of aid to the Malagasy government (Schwitzer et al., 2013; Schwitzer et al., 2014). Most people on the island live on less than $1.25USD per day and suffer from malnourishment with limited protein sources available to them (Waeber, Wilmé, Mercier, Camara, & Lowry, 2016).

There are simply not enough resources to enforce protection of lemurs and habitats, and there is a strong incentive to hunt lemurs either to directly feed families or gain some sort of income by selling to the bushmeat trade (Schwitzer et al., 2013). It can feel impossible to effectively protect lemurs without significant work occurring within local communities and economic sectors.

While conservation in the field is critical, captive lemurs can provide a host of information to be utilized in the wild as well as to improve enrichment and enclosure design in captive lemurs. Learning about their behavior and physiology can aid conservation efforts in the wild as we understand how best to protect extant lemur species and their needs. For example, if we understand how primates respond to novel environments and situations, we can better predict how a species may respond to environmental change or even translocation, which may be necessary in the future as environmental conditions and habitats continue to degrade. Thus, captive research can aid conservation in the field as well as improve the well-being of captive individuals.

Social Organization

Ring-tailed lemurs, the most commonly studied of all lemur species, share more traits with Old World monkeys than expected despite diverging 64 to 87 million years ago (Herrera & Dávalos, 2016; Perelman et al., 2011). Like cercopithecines, social groups are generally multi-male, multi-female, with females remaining in their natal groups for life while males disperse to different groups when they reach adulthood (Goodman, Rakotoarisoa, & Wilmé, 2006; Nakamichi & Koyama, 1997). In addition, the female dominance hierarchy falls into a matriline, where mothers are dominant over daughters (Nakamichi and Koyama, 1997; Goodman et al., 2006). In contrast to cercopithecines, many lemurs, including ring-tailed lemurs, exhibit female dominance. While other primate taxa exhibit female dominance, such as bonobos (*Pan paniscus*), it is more common in the Lemuriformes (Lewis, 2018). In the wild, troops of ring-tailed lemurs average 12-15 individuals, though troops of up to 30 have been spotted. A central dominant female will initiate and determine group movement, which often occurs on the ground, as ring-tailed lemurs are semi-terrestrial. Dominant females also receive priority feeding and grooming (Jolly, 1966; Sauther & Sussman, 1993). Females are generally the sex that takes the most active part in aggression between troops (Kittler & Dietzel, 2016). While males have their own dominance hierarchies, females will mate with males of any rank despite males participating in mate guarding, though subordinate males tend to live on the periphery of groups (Jolly, 1998).

Though captive red ruffed lemurs also exhibit a clear hierarchy with females dominant over males, it is not quite as strictly linear as that of ring-tailed lemurs and aggression levels are much lower in red ruffed lemur societies (Vasey, 2006). In the wild, their dominance hierarchy and the extent of female dominance is less clear than in captivity (Lewis, 2018; Vasey, 2006). Wild red ruffed lemurs, who are highly arboreal, have a fission-fusion social system, similar to that of chimpanzees (*Pan troglodytes*), in which a large group divides into subgroups whose members independently forage and move throughout the day so that, though the entire group shares a home range, all group members are rarely seen together (Vasey, 2006). Low aggression levels also mean that red ruffed lemurs are more socially tolerant of each other and will allow other groupmates close enough to them to observe object manipulations or feeding strategies (Fitchel, Schnoell, & Kappeler, 2017).

Social Diffusion of Information

Social diffusion is the transfer of information from one individual to another (Dindo, Thierry, & Whiten, 2008). The single female Japanese macaque (*Macaca fuscata*) who spontaneously acquired a potato washing behavior that then spread throughout her social group is a prime example of social diffusion (Kawai, 1965). Learning novel techniques from conspecifics could prove critical if food or water is limited in the habitat, and some individuals may be unable to acquire this behavior on their own. For example, wild red-fronted lemurs (*Eulemur rufifrons*) take fewer trials to successfully open a box if they have watched experienced individuals succeed at the task (Schnoell & Fichtel, 2012). This type of social learning occurs in many other primates, including squirrel monkeys (*Saimiri* spp.) (Claidière, Messer, Hoppitt, & Whiten 2013; Dean, Hoppitt, Laland, & Kendal, 2011), ring-tailed lemurs (Kendal et al., 2010), black-and-white ruffed lemurs (*Varecia variegata*) (Stoinski, Drayton, & Price, 2011), and vervets (*Chlorocebus pygerythrus*) (Botting, Whiten, Grampp, & van de Waal, 2018).

Ring-tailed lemurs have a more linear dominance hierarchy than other lemur species (Sauther & Sussman, 1993), which may influence social learning and how information diffuses throughout a group. In the wild, they are known to be less socially tolerant than other lemur species. The probability of any single ring-tailed lemur in a group feeding on a clumped resource is much lower than that of the more egalitarian red-fronted lemurs, because dominant ring-tailed lemurs will not allow subordinates close enough to interact. Thus, in most social learning experiments, only subgroups of ring-tailed lemurs will learn a particular task (Fichtel, Schnoell, & Kappeler, 2017). However, aggression in ring-tailed lemurs typically occurs around limited resources, so learning in subgroups may be limited to situations lacking competition. The captive lemurs who spontaneously began drinking water from their tails by observing each other did not need this behavior to acquire water, as they had plenty available from other provided sources (Hosey, Jacques, & Pitts, 1997). In this case, dominant individuals did not have to fight for water access, so they may have allowed subordinates close enough to observe and practice the behavior whereas in the wild, they may have become aggressive if a subordinate attempted to approach on the limited resource. Captive lemurs may be able to observe behavior of conspecifics more easily because most of their resources are not limited to the way they are in the wild and, thus, dominant individuals may be more socially tolerant (Fichtel et al., 2017), as evidenced by the lower rates of aggression that are typically observed in captive ring-tailed lemur populations, barring significant sources of stress (Dye, 2017; Tarou, Bloomsmith, & Maple, 2005).

Primates in Captivity

Captive primates utilize different substrates and components of their enclosures for varying purposes. For example, the addition of a large vertical structure into a chimpanzee enclosure appeared to be used by chimpanzees specifically to escape aggression (Caws, Wehnelt, & Aureli, 2008). Captive primates also do not often use the entirety of their enclosures; gorillas (*Gorilla beringei*) have been observed spending 50% of their time in less than 15% of their enclosure (Stoinski, Hoff, & Maple, 2001) and, if designed thoughtfully, orangutans (*Pongo pygmaeus*) will favor the upper canopy of an enclosure (Malone, 1998; Hebert & Bard, 2000). In fact, several primate studies have shown that the complexity of the space is more important for welfare—the physical and mental health of an animal—than its size, especially for highly arboreal primates (Hosey, 2005; Tarou et al., 2005; Webb, Hau, & Schapiro, 2018). Chimpanzee behavior does not differ significantly between enclosures of different sizes if the complexity is kept relatively equal (Reamer et al., 2015; Webb et al., 2018). In enclosures that are not complex enough, lion-tailed macaques (*Macaca silenus*) will utilize the edge of the enclosure more frequently, and this is also the area where they exhibit the most abnormal behaviors (Mallapur, Waran, & Sinha, 2005). However, this does not mean that the amount of space available to an animal is never important; decreased spatial availability has been linked to an increase in cortisol levels in ungulates (e.g., *Cervus* spp., *Diceros* spp.) (Li, Jiang, Tang, & Zeng, 2007).

Enclosures require money and careful design, along with frequent upkeep, so it is important to know how primates are utilizing their environments and what aspects are most critical to include for a particular species. If natural lion-tailed macaque habitat is degraded enough, they are likely to behave in a similar fashion to their captive counterparts and utilize edge habitat more often (Mallapur et al., 2005). Furthermore, differences in behavior between captive and wild ring-tailed lemurs appear to be primarily related to activity budgets (Shire, 2012) so, while the relative proportion of activities differs between captivity and the wild, most observed behaviors could be quite similar to those in the wild even if they are occurring in different contexts. For example, captive lemurs displayed more species-specific behaviors, but they had an overall lower frequency of agonistic encounters than wild lemurs, and spent a larger portion of their time resting than wild lemurs (Shire, 2012).

Ring-tailed lemurs are the most commonly found lemur in zoos and generally thrive in captivity. Infant mortality rates are low, breeding success is high (Mason, 2010), and the prevalence of stereotypic behaviors, or abnormal repetitive behaviors lacking a goal or function (Hosey, 2005), have been recorded between two and six percent (Dye et al., 2017; Tarou et al., 2005). Abnormal behaviors do not seem to occur frequently, suggesting that behaviors in captivity may mirror ring-tailed lemurs' natural behaviors. While many enrichment items given to captive primates may not be encountered anywhere in their natural environment, they could still stimulate naturalistic behaviors. Furthermore, the presence of natural, or species-typical behaviors, are generally used as a benchmark to assess captive animal welfare and wellbeing (Hosey, 2005).

Object Use in Primates

Man-made foraging devices are a popular way in both zoos and laboratories to increase activity and naturalistic behavior. These can be made of polyvinyl chloride pipes, wooden or plastic puzzle boxes, cardboard, and many other types of material (Shapiro, Shapiro, & Ehmke, 2018). Each type of foraging device requires different methods to manipulate and open or gain access to the food inside, and not every lemur will manipulate it the same way. Ring-tailed lemurs, for example, will more often attempt to use or open devices from the ground than other species, perhaps because they are the most terrestrial of all lemurs (Shapiro et al., 2018). The more arboreal sifakas and ruffed lemurs, however, prefer to climb and even hang upside down to manipulate devices that are not on the ground (Shapiro et al., 2018). This is especially significant in captive environments because animals may be encouraged to utilize more available space by placing foraging materials or other enrichment of interest in certain places of an enclosure. Furthermore, data indicate that increasing the presence of objects primates can manipulate can decrease the frequency of stereotypic behaviors (Kerridge, 2005).

While differences in how particular species manipulate objects and their environment is to be expected, there are also differences between individuals. For example, as noted previously, a novel behavior was observed in ring-tailed lemurs at a zoo, wherein they spontaneously began using their tails to drink water from the moat surrounding their enclosure. However, each lemur performed this behavior in a slightly different way (Hosey et al., 1997). When separated and taught two different methods of opening an artificial feeding box, vervets brought back together did not conform to one method, and naive individuals learned both methods without a preference for one or the other (Botting et al., 2018). A similar study in capuchins (*Cebus apella*) yielded comparable results; capuchins also did not conform to one method and, in fact, seemed to pay more attention to the rarest methods of opening food boxes (Barrett, McElreath, & Perry, 2017). Thus, primates can operate independently of each other and achieve goals or manipulate objects in different ways, even when in the same social group; the group does not have to conform to a single method.

Of importance to the current proposed research, a field study by Russon, Kuncoro, Ferisa, and Handayani (2010) identified 44 different variants of water use in wild orangutans over a sampling period of 20 months, including 18 probable innovations. Orangutans used water for several purposes, including playing, traveling, drinking, and social interactions (Russon et al., 2010). In that study, behavioral descriptions were very specific, including what type of object (if any) was used with the water and the direct steps the orangutan took, such as picking up a stick, reaching it towards an object in the water, and using the stick to move an object such as a leaf closer to them.

After examining the ways in which orangutans used a water source, Russon et al. (2010) categorized the contexts in which water use occurred, including water-related travel, social use of water, and using water for play behaviors. For orangutans, water use may serve multiple purposes as suggested by the varied contexts in which use occurred. This may also be true of lemurs, in that substrates and objects in their environments may be utilized for many different purposes in addition to their original intended use or function. Studies about object use in primates have primarily related to social learning and enrichment preferences in captivity (e.g., Barrett et al., 2017; Claidière et al., 2013; Dindo et al., 2008; Gronqvist, Kingston-Jones, May, & Lehmann, 2013; Shapiro et al., 2018). To my knowledge, no study similar to Russon et al. (2010) has examined categories or contexts in which object and environmental use frequently occur in lemurs.

Study Goals and Hypotheses

The primary aims of this study were to 1) develop a catalogue of environmental/object use in captive ring-tailed and red ruffed lemurs, 2) identify the most common contexts in which lemur environmental/object use occurs, 3) identify the most common behavioral categories captive lemurs perform, 4) determine whether captive lemurs utilize all areas of their enclosures, and 5) compare enclosure use between a more terrestrial lemur species, the ring-tailed lemurs, and a highly arboreal species, the red ruffed lemurs. I expected that both ring-tailed and red ruffed lemurs would spend the majority of their time engaging in inactive behaviors, that they would interact in some way with each substrate in their respective enclosure, and they would utilize each section of their large outdoor enclosures.

CHAPTER III

METHODS

Participants

Lemurs. During data collection, the zoo housed five adult male ring-tailed lemurs and two male and one female adult red ruffed lemurs on public exhibit. Details on these lemurs can be found in Table 1. Ages stated are the ages that the lemurs were when I began data collection. I spent several days learning to identify each lemur with the assistance of a zookeeper before I began collecting data. The bachelor group of ring-tailed lemurs were all related to each other; Reese fathered each of the remaining four in the group. Tahiry and Cash were full siblings while the others were half siblings. Lucienne and Orion, the two male red ruffed lemurs, were twins, while Sally, the only female, was unrelated as she was brought to the zoo from the Duke Lemur Center for breeding purposes.

Table 1

Demographics of Lemurs Observed at the Woodland Park Zoo

Name	**Species**	**Age (yrs)**	**Sex**	**Date of arrival at Woodland Park Zoo**
Sally	*Varecia rubra*	3	F	30 Apr 2019
Orion	*Varecia rubra*	12	M	25 Apr 2012
Lucienne	*Varecia rubra*	12	M	23 May 2012
Bucky	*Lemur catta*	4	M	22 Apr 2015
Reese	*Lemur catta*	11	M	22 Apr 2015
Tamole	*Lemur catta*	5	M	22 Apr 2015
Tahiry	*Lemur catta*	5	M	22 Apr 2015
Cash	*Lemur catta*	6	M	22 Apr 2015

Materials

Study site. I conducted research at the Woodland Park Zoo in Seattle, Washington. During data collection, the lemur habitats at the Woodland Park Zoo were both large outdoor areas full of large trees and terrain that could make it difficult to spot the specific behaviors a lemur was performing. Thus, I used binoculars to allow for the most accurate observations possible. Both habitats contained bodies of water along the edges, several large rocks, and trees. The ground was covered in grass, shrubbery, and large logs that the lemurs were able to walk across. The ring-tailed lemur habitat also contained three hammocks several meters off the ground, while the red ruffed lemur habitat contained one hammock and a few cave-like structures in the front portion of the habitat. Each enclosure had an artificial waterfall which zoo staff confirmed were designed to help mask external noise. Both species also had access to indoor areas that were not visible to visitors or to me during my observations (see Appendix A for diagrams of each enclosure).

The ring-tailed and red ruffed lemur habitats were next to each other, each allowing for visitors to view the animals from two or three different angles. At times, lemurs could be obscured by hills or rocks in the enclosures, or they could be located outside of the viewing area. Data collection occurred from corners of the viewing areas so as not to disturb visitors; I selected different corners depending on the need to sample specific individuals (see Appendix A). I provided visitors who asked me questions during data collection with a pamphlet from the Central Washington University's Primate Behavior and Ecology program with an indication that I was conducting research.

Procedures

Focal samples. For data collection, I performed 5-minute focal samples (Altmann, 1974). Each lemur was assigned a number that I placed into a random number generator every morning to determine the order in which sampling would occur, with the following criteria: 1) All eight lemurs must be assessed before repeating any individual, and 2) focal samples for individual lemurs were varied in their order so that no lemur was sampled after the same animal twice on a given day. Combining the two species in this generator allowed me to obtain focal samples at different times of the day for both species. The set of eight lemurs was assessed four times per day, twice between 9:45 am and 12:30 pm and twice in the afternoon between 12:45 pm and 4:30 pm, from July 27th, 2019 to September 18th, 2019 for a total of 22 days of data collection. Each lemur was observed for a total of 88 focal samples.

During focal samples, I recorded several pieces of information on each lemur's behavior via an audio device, which I transcribed at the end of data collection. When the focal animal interacted with any physical object or substrate, I collected the following information about the interaction: 1) Identity and species of the focal lemur; 2) location of the focal lemur within the enclosure; 3) the object/substrate the animal was interacting with; 4) how the animal was utilizing or using the object/substrate; and 5) proximity of other lemurs to the focal individual. At times, the specific behavior of a lemur was not visible, although I could record where in the enclosure the lemur was located; if lemurs were in the trees, foliage often blocked views of what behaviors the lemurs were performing. More detail regarding the specific information that was recorded is provided in the following paragraphs.

The level of detail I recorded when collecting behavioral data was similar to that found in Russon et al. (2010), wherein I recorded the specific variants of behaviors (i.e., whether an object was being manipulated only by an animal with their hands or if they are sniffing an object, if two legs or all four are being used, if an object was being thrown or torn, if they are eating an object, or anything else they are doing with it). For the location of the lemur, the enclosure was divided into vertical heights: Ground (G), mid-level (M), or high (H). It was also divided into sections based on location of the lemur from the visitor's point of view: Front-right (FR), front-left (FL), back-right (BR), back-left (BL), and central (CENT). Both the ring-tailed and red ruffed lemur habitats contained an approximately central grove of trees that was used to determine these locations. A lemur that was past the right and front edge of this grove of trees was marked as front-right, from the right and back edge of the grove as back-right, etc. A lemur with all four limbs on the ground was recorded as located on the ground, no limbs on the ground but below 4.5 meters as mid-level, and above 4.5 meters as high. To determine this height when collecting data, artificial bamboo bridges in each enclosure were used, as they were approximately 4.5 meters off the ground. This information was collected to assist in determining if lemurs were utilizing the entirety of their enclosures.

The object or substrate the lemur was utilizing during each behavior was also included. Substrates included the following: rocks, ground, hammock, tree, branch on ground (in the case of a branch that is not attached to a tree), duck box, bamboo bridge, cave, log bridge, and bush. Finally, proximity of other lemurs to the focal individual was noted as a measure of sociality. The number of lemurs within arm's reach of the focal lemur was determined to be in proximity, while any animal outside of arm's reach was not in proximity. The only time this method was not employed was if lemurs were huddling—the entire group of five ring-tailed lemurs often huddled together and, in this case, the entire huddle was considered to be in proximity to the focal lemur, regardless of the focal lemur's location within the huddle.

Table 2

Background Behavioral Ethogram

Behavioral Category	**Included Behaviors**
Inactive	• Sitting, inactive (not engaging with any other lemurs or objects, no abrupt movements) • Self-huddle (Head curled in on chest with body in the shape of a ball, tail hanging down or wrapped around body) • Laying on stomach with limbs dangling off branch, inactive (not engaging with any other lemurs or objects, no abrupt movements) • Laying on side, inactive (not engaging with any other lemurs or objects, no abrupt movements) • Sunning (the lemur, sitting, faces ventrally towards the sun with legs extended out in front of itself)
Social	• Huddling (body is in contact with at least one other lemur, lemurs are not locomoting or otherwise moving) • Allogroom (initiate groom, receive groom, or initiate while receiving groom) • Swat conspecific with hand
Foraging	• Sniffing or reaching for any potential food object (leaf, twig, primate chow, vegetable, fruit, flower bud, grass) with one or both hands • Pushing nose through grass in a forward motion • Licking rocks • Reaching for branches and/or leaves, then letting go without placing in mouth

Table 2 (Continued)

Behavioral Category	Included Behaviors
Locomotion: Must move at least 1m away from starting location	• Bipedal or quadrupedal jumps/leaps • Walking • Climbing on any surface
Not Visible	• Unable to visually determine the location or behavior
Feeding	• Chewing or placing any potential food object in mouth (leaf, twig, primate chow, vegetable, fruit, flower bud, grass)
Vigilance: Abrupt head movement accompanied by a glance lasting at least 1 second	• Vigilance towards visitors, planes, birds, conspecifics, or unknown
Miscellaneous	• Self-scratch • Yawn • Scent-marking (rubbing wrists, chests, cheeks, or anogenital region against trees, branches, or rocks repeatedly)

Analyses. Three undergraduates transcribed the audio recordings word-for-word into Excel. Data analysis for this study is descriptive and, thus, no inferential statistics were conducted. During each focal sample, each time the lemur changed from one behavior to another, it was recorded as a new discrete behavior. Therefore, in one focal sample, I may have recorded one single behavior if the lemur was, for example, huddling for the entire focal, or I may have recorded several behaviors if a lemur was, for example, walking, then started foraging, and then went back to walking. As such, to assess substrate use and spatial use, all data were converted to proportions based off the total number of discrete behaviors recorded for each species. To assess activity budgets, all discrete recorded behaviors were grouped according to the categories found in Table 2 and then converted to proportions based on the total number of discrete behaviors recorded for each species. For ring-tailed lemurs, 2,428 total discrete behaviors were recorded. For red ruffed lemurs, 1,888 total discrete behaviors were recorded.

CHAPTER IV

RESULTS

The angles available for viewing lemurs as well as the denseness of the foliage made viewing the specific actions of the lemurs difficult when they were further back in the enclosure or high in the canopy. Subsequently, I was not able to reliably determine environmental use to the level of detail I had expected (e.g., whether lemurs were using one or two hands to hold something or the specifics of how they foraged for food). However, by grouping behaviors into the categories presented in Table 2, I was able to discern valuable information about the lemurs' activity budgets and enclosure use.

Spatial Use

Height. Of 2,428 discrete behaviors recorded, the ring-tailed lemurs performed 42.0% (n = 1019) of behaviors on the ground, 50.2% (n = 1219) at the mid-height level, and 5.2% (n = 126) at the high level. Ring-tailed lemurs were not visible for 5.5% (n = 133) of recorded behaviors pertaining to height. Of 1,888 discrete behaviors recorded, the red ruffed lemurs performed 23.0% (n = 434) of behaviors on the ground, 54.0% (n = 1,020) at the mid-height level, and 20.3% (n = 383) at the high level. Red ruffed lemurs were not visible for 4.5% (n = 84) of scans pertaining to height. These results are summarized in Figure 1.

Location. Of 2,428 discrete recorded behaviors, the location for ring-tailed lemurs was unknown or the lemurs were not visible for 9.7% (n = 236) of the instances of recorded behavioral observations. The ring-tailed lemurs performed 34.5% (n = 838) of behaviors in the back-left, 5.5% (n = 135) of behaviors in the back-right, 5.2% (n = 127) of behaviors in the front-right,

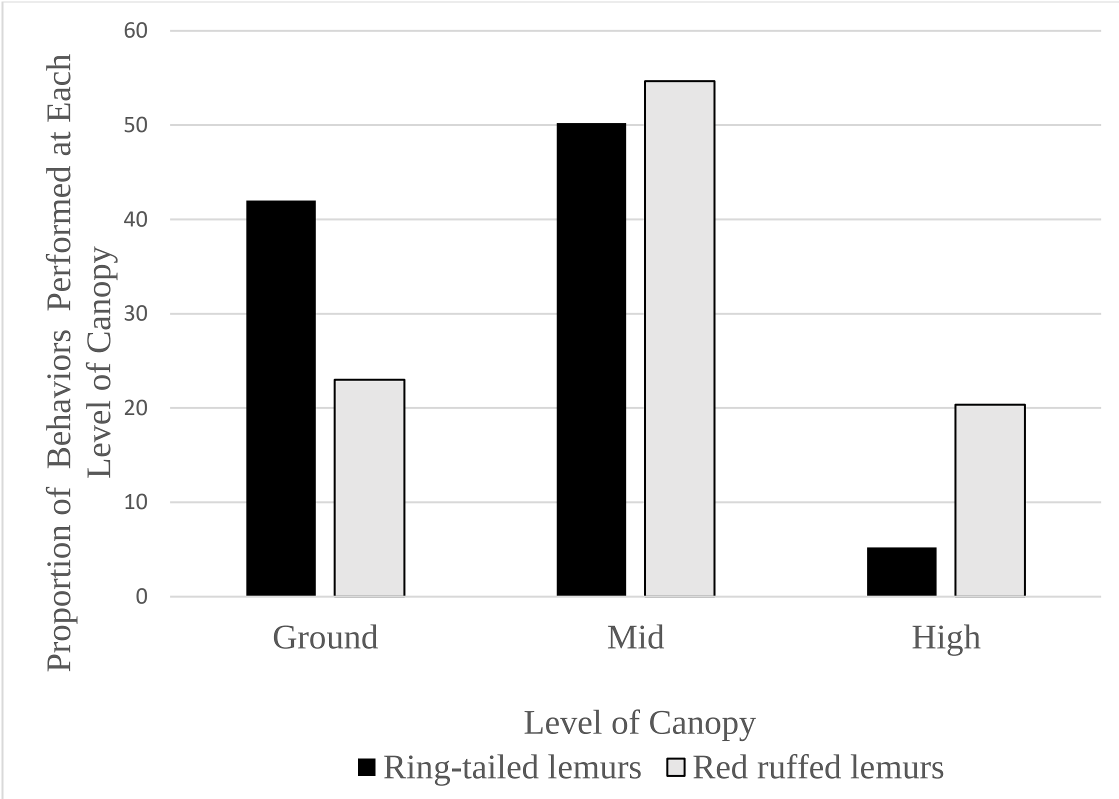

Figure 1. Proportion of behaviors spent at different heights of the canopy.

18.9% (*n* = 460) of behaviors in the front-left, and 26.0% (*n* = 632) of behaviors in the central area of their outdoor enclosure.

Of 1,888 discrete recorded behaviors, red ruffed lemur location was unknown or the lemurs were not visible for 15.9% (*n* = 300) of the instances of recorded behavioral observations. Red ruffed lemurs performed 9.6% (*n* = 180) of behaviors in the back-left, 34.4% (*n* = 649) of behaviors in the back-right, 35.8% (*n* = 676) of behaviors in the front-right, 2.9% (*n* = 55) of behaviors in the front-left, and 1.5% (*n* = 28) of behaviors in the central area of their outdoor enclosure. These results are summarized in Figure 2.

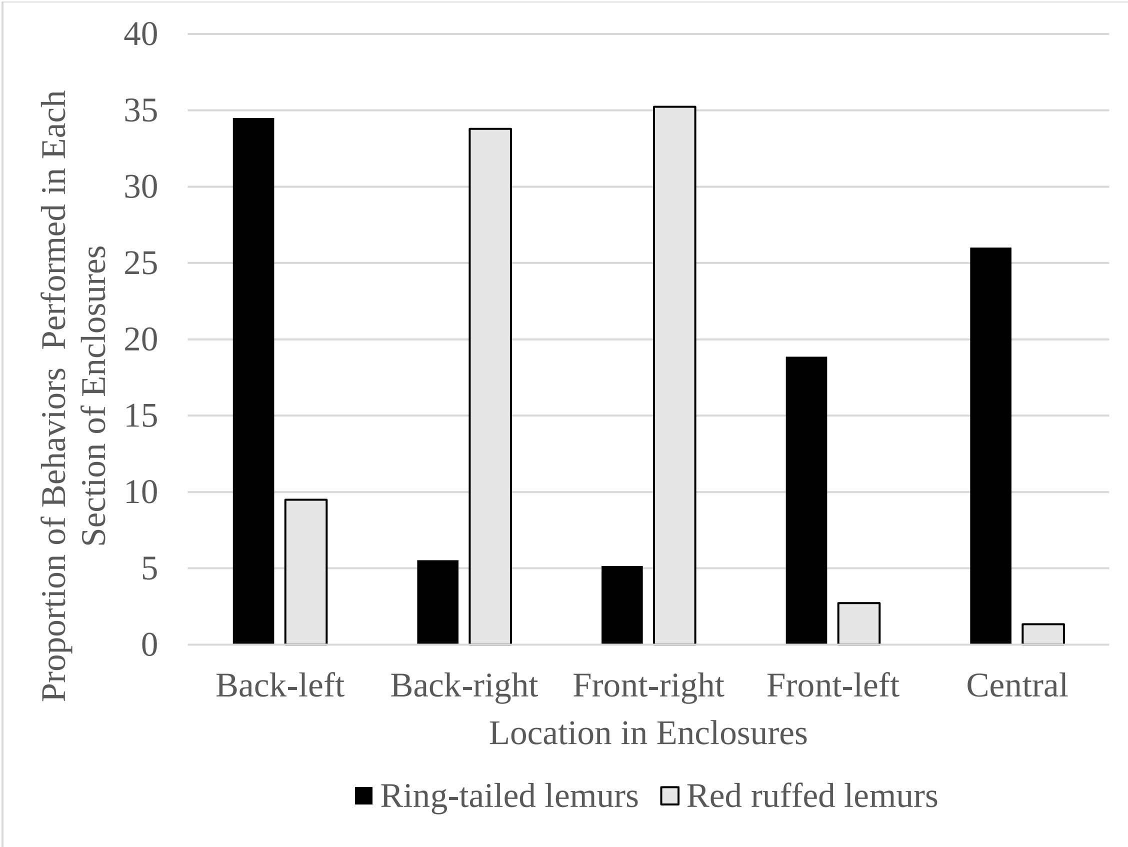

Figure 2. Proportion of behaviors spent in each section of ring-tailed and red ruffed lemur enclosures.

Substrate Use

Of 2,428 discrete behaviors recorded, the substrate used most frequently by ring-tailed lemurs was the ground, accounting for 42.5% (n = 1,032) of behaviors. Following the ground, the substrate used most frequently was hammocks, accounting for 26.2% (n = 636) of behaviors. Trees accounted for 19.1% (n = 464) of behaviors, after which other substrates were not used very frequently. Their least used substrate was the duck box, accounting for 0.1% (n = 3) of behaviors.

The red ruffed lemur enclosure lacked a few substrates that the ring-tailed lemur enclosure contained, specifically bushes, a platform, and the duck box. In contrast to the ring-tailed lemurs, of 1,888 discrete recorded behaviors, the most utilized substrate for red ruffed lemurs were trees, accounting for 68.4% (n = 1,291) of behaviors while the ground accounted for 16.7% (n = 315) of behaviors. Red ruffed lemurs utilized their hammock for just 0.1% (n = 2) of behaviors. They also utilized other substrates on the ground, such as logs, rocks, and bridges, slightly more than ring-tailed lemurs. Results of all substrate use are presented in Table 3.

Table 3

Percentage of Discrete Recorded Behaviors Spent Utilizing Each Substrate

Substrate	**Ring-tailed lemurs**	**Red ruffed lemurs**
Ground	42.5 (n = 1032)	16.7 (n = 315)
Tree	19.1 (n = 464)	68.4 (n = 1291)
Hammock	26.2 (n = 636)	0.1 (n = 2)
Branch on ground	1.5 (n = 36)	2.7 (n = 51)
Bush	3.2 (n = 78)	N/A
Rock	0.6 (n = 15)	4.8 (n = 91)
Log bridge	0.7 (n = 17)	3.7 (n = 70)
Bamboo bridge	0.8 (n = 19)	0.5 (n = 9)
Platform	0.7 (n = 17)	N/A
Cave	1.6 (n = 39)	0.9 (n = 17)
Duck box	0.1 (n = 3)	N/A
Ropes	0.9 (n = 23)	0.1 (n = 2)
Not visible	2.0 (n = 49)	2.1 (n = 40)

Activity Budgets

Both ring-tailed and red ruffed lemurs spent the majority of discrete recorded behaviors in an inactive state, with inactivity accounting for 32.8% (*n* = 796) of 2,428 recorded ring-tailed lemur behaviors and 30.4% (*n* = 574) of 1,888 recorded red ruffed lemur behaviors. For ring-tailed lemurs, vigilance behaviors followed inactivity in frequency, accounting for 22.2% (*n* = 539) of their behaviors. For red ruffed lemurs, locomotion followed inactivity, accounting for 25.4% (*n* = 480) of their behaviors. Vigilance accounted for 8.3% (*n* = 157) of red ruffed lemur behaviors. Activity budget data are summarized in Table 4. The difference in visibility between activity budget data and substrate use data is due to occasional difficulties in observing what the lemurs were actually doing—there were times when I could see where in the enclosure the lemur was, but the foliage might have been dense enough that I could not see what behaviors they were performing.

Table 4

Each Behavior Category as a Percentage of the Overall Behavioral Repertoire Observed

Behavior Category	**Ring-tailed lemurs** (%)	**Red ruffed lemurs** (%)
Inactive	32.8	30.4
Vigilance	21.6	8.2
Locomotion	11.6	25.4
Social	11.8	7.2
Miscellaneous	9.1	12.3
Feeding	4.5	6.1
Foraging	3.5	5.6
Not visible	5.5	5.0

CHAPTER V

DISCUSSION

Both ring-tailed and red ruffed lemurs performed the majority of behaviors at the mid-height level of the canopy and showed the least percentage of behaviors at the high points of the canopy. Ring-tailed lemurs rarely used the right side of their enclosure, mostly preferring the left side or the central area. Red ruffed lemurs rarely used the left side of their enclosure, preferring the right side. Ring-tailed lemurs primarily used the ground as a substrate while red ruffed lemurs primarily used the trees. Ring-tailed lemurs frequently used the hammocks when they were off the ground, while red ruffed lemurs only used their hammocks a total of three times during data collection. Both species spent very little time foraging and feeding, spending most of their time engaged in inactive behaviors. In addition to inactivity, ring-tailed lemurs engaged in vigilance behaviors very often. Red ruffed lemurs also frequently engaged in vigilance behaviors, although to a lesser degree than ring-tailed lemurs.

Spatial Use

Neither species of lemur in this study utilized all the space available to them in the enclosure space that was visible to visitors. The ring-tailed lemurs rarely used the right side of their enclosure, while the red ruffed lemurs rarely used the left side of their enclosure. Furthermore, both species had the majority of their behaviors recorded at the mid-height level of the canopy and the least percentage of their behaviors recorded at the high level of the canopy. Preferences for specific features or areas of their enclosure have been previously reported in zoo animals (Mallapur et al., 2005; Stoinski et al., 2001). Although zoo enclosures are expensive to design and upkeep is required, an animal not utilizing the entirety of its enclosure may not be a concern in some cases and may reflect their naturally-occurring behavioral patterns. For example, orangutans, who are highly arboreal species in the wild, will favor the upper canopy of their enclosures if designed according to the behavioral ecology of orangutans (Hebert & Bard, 2000).

However, limited space is often detrimental to captive species. Fecal cortisol levels, indicative of stress, are higher in captive Père David’s deer stags (*Elaphurus davidianus*) when they live in a small area compared to when they live in a free-ranging area (Li et al., 2007), and decreased space is linked to higher cortisol levels and decreased reproduction in many species, including black rhinoceroses (*Diceros bicornis*), macaques (*Macaca* spp.), and ungulates such as elk (*Cervus* spp.) (Carlstead & Brown, 2005; Crockett, Shimoji, & Bowden, 2005; Del Thompson, 1989). Captive chimpanzees exhibit a decrease in stereotypic behaviors and an increase in activity when moved to larger enclosures (Brent, Lee, & Eichberg, 1991; Clarke, Juno, & Maple, 1982). Therefore, it is most often desirable to provide captive animals with a larger area of space, while still considering the complexity requirements of the animal.

The spatial use observed in red ruffed lemurs in the current study does not mirror behavior typically observed in the wild. In the wild, red ruffed lemurs are highly arboreal and do not often come down to the ground (Vasey, 2005). The red ruffed lemurs in this study performed 20% of behaviors high in the canopy whereas 23% of their observed behaviors were performed on the ground. If enclosure design at zoos is, at least in part, designed to simulate the natural environment, then red ruffed lemurs should be spending most of their time high in the canopy; although captive black-and-white ruffed lemurs are also known to spend significant amounts of time on the ground despite being almost exclusively arboreal in the wild (Kerridge, 2005). There are several possible reasons that the red ruffed lemurs at the Woodland Park Zoo had a lower proportion of their behaviors observed high in the canopy.

One potential reason for these captive lemurs performing few behaviors in the upper canopy may be that foliage in the high parts of the canopy was sparser than the species' preferred coverage. Both chimpanzees and gorillas in captive environments avoid open spaces when they live in sparser enclosures (Ross, Schapiro, Hau, & Lukas, 2009). Given that wild ruffed lemurs are susceptible to aerial attacks from raptors (Sauther, 1989) and have, thus, evolved anti-predator strategies because of this (Karpanty & Wright, 2007), the captive lemurs in this study may have felt too exposed and thus performed most behaviors in the area of the enclosure that provided more protection in the form of denser foliage. In a playback study conducted in the wild, Milne-Edward's sifakas (*Propithecus edwardsi*) and Eastern lesser bamboo lemurs (*Hapalemur griseus*) moved to lower portions of the canopy when presented with aerial predator calls (Karpanty & Wright, 2007). While no aerial predators were spotted at the Woodland Park Zoo during data collection, and there are no records of predation on the lemurs there, predator avoidance is an evolutionary behavior (Karpanty & Wright, 2007) and thus may be driving the red ruffed lemurs to perform most behaviors lower in the canopy where, in the wild, they would be less susceptible to predation.

There are somewhere between 1,800 and 2,500 lemurs in captivity in zoos around the world (Andriaholinirina et al., 2014a), but published data examining vertical spatial use in captive ring-tailed lemurs appears to be rare. In one study, Hedge (2005) found that a group of three ring-tailed lemurs at a zoo spent approximately 50.0% of their time in the trees and approximately 40.0% of their time on the ground. Research on wild populations suggests that ring-tailed lemurs spend around 33.0% of their time on the ground (Sussman, 1999). The ring-tailed lemurs at the Woodland Park Zoo in this study performed 42.0% of recorded behaviors on the ground, which is consistent with previous research on this topic. This highlights the importance of ground substrate in captive ring-tailed lemur enclosures. As a semi-terrestrial species, ring-tailed lemurs naturally spend a significant amount of their day on the ground. A more natural ground substrate in captivity allows the lemurs to exhibit their natural behaviors, such as foraging, on the ground as they would in the wild.

Ring-tailed lemurs at the Woodland Park Zoo performed approximately 55.0% of recorded behaviors off the ground, though less than 6.0% of this occurred at the high point of the canopy. In contrast to the red ruffed lemur enclosure, the highest points of the canopy in the ring-tailed lemur enclosure were covered with dense foliage. However, when feeding on tamarind trees, ring-tailed lemurs in the wild split their time evenly between open and closed areas of the canopy (Mertl-Millhollen et al., 2003). It is, therefore, unlikely that the openness (or lack thereof) influenced the ring-tailed lemurs to stay away from the highest points in the trees. I could not find published data on how high ring-tailed lemurs typically climb in the wild but, as they are known to spend so much time on the ground, it is likely that the limited use of the highest points in their enclosure by the ring-tailed lemurs in this study is not atypical for the species.

Despite the presence of a hammock, a substrate the ring-tailed lemurs used often, on the right side of their enclosure, the ring-tailed lemurs performed just 10.7% of recorded behaviors on that side of their enclosure. They only seemed to venture to the right side of their enclosure when the keeper placed food in that area where there was one feeder raised off the ground. The waterfall, meant to mitigate external noise, was located on the right side of their enclosure. While it is possible that the lemurs wanted to avoid this waterfall, this seems unlikely, as the red ruffed lemurs performed nearly all recorded behaviors on the right side of their enclosure, which is where their waterfall is also located. While there is no evidence of lemurs swimming (Goodman & Ganzhorn, 2003), captive ring-tailed lemurs will approach and interact with bodies of water in their enclosures (Hosey et al., 1997). Furthermore, zookeepers reported that Sally, the female red ruffed lemur in this study, tried to leap out of the enclosure one morning and landed in the water near the beginning of the data collection period. She was able to walk through the water and return to her enclosure without apparent difficulty. She did not noticeably change her behavior in any way after this incident, except that she no longer tried to escape the enclosure. While it does not appear that captive lemurs are averse to water, it is a possibility that these specific ring-tailed lemurs were more hesitant to spend time near the waterfall.

Both species avoided the section of their enclosures that are closest to the other species. In the wild, ring-tailed and red ruffed lemurs are not sympatric with one another, although they are sympatric with others from the Lemuridae family (Jolly, 1966). The lemurs at the Woodland Park Zoo would have been able to see each other if they were somewhere at the midpoint of the canopy on the adjacent sides of their enclosures. While these species do coexist in mixed-species groups in captivity across the world, if given the choice, the current data suggest that they may be choosing to avoid or are wary of one another in captivity; a finding with ramifications for enclosure design for captive animals.

Shire (2012) found that, while interactions between a cohabitating group of ring-tailed and red ruffed lemurs were infrequent, both species were experiencing stress related to the presence of the other species and exhibited agonistic behaviors toward one another.

In addition, both species in this study tended to stay on the side of their enclosure that was closest to their entrance to the indoors. It seems unlikely that this was due to stress caused by visitors; the animals always had the option to go inside, away from the view of visitors, but the animals were outside nearly every day of data collection. I rarely saw food being provided by keepers on the side of the enclosure that the lemurs did not prefer, so it is possible that their reluctance to leave the area was related to being near food. Spacing food throughout the enclosure could provide benefits by increasing foraging time for the lemurs to better match their wild habits while also increasing their use of the space available to them. If the lemurs continue to avoid specific areas, even in the presence of food, it may be beneficial to feed the two species at different times so that they are not forced to be in adjacent areas of their enclosures at the same time. Finally, the height of the canopy on the left side of the red ruffed lemur enclosure was significantly lower than the height on the right side. This may have influenced the lack of use of the left side of their enclosure by the red ruffed lemurs. However, given that they performed a limited amount of behaviors at the high point of the canopy even on the right side of the enclosure, these data suggest that it might be more important to provide sufficient canopy coverage across an enclosure rather than an equal distribution of canopy height.

Substrate Use

The two species differed in their most frequently used substrate; ring-tailed lemurs used the ground most often, while red ruffed lemurs used trees. The ring-tailed lemurs seemed more comfortable directly using the ground, whereas the red ruffed lemurs tried to avoid the ground more often, accounting for their slightly higher use of rocks, log bridges, and branches. Given their ecology, with ring-tailed lemurs being semi-terrestrial and red ruffed lemurs highly arboreal, these results were not unexpected and appear to mimic each species' natural behavior (Jolly, 1966; Vasey, 2005).

Ring-tailed lemurs in this study frequently used the hammocks in their enclosure, whereas the red ruffed lemurs very rarely used the hammock in their enclosure. The simplest explanation for this is the number of hammocks available—the ring-tailed lemurs had three throughout their enclosure, while the red ruffed lemurs only had one. However, it appears that placement of the hammocks may have played a role in their differential patterns of use. Of the three hammocks, the ring-tailed lemurs frequently used two. The third hammock was located on the right side of their enclosure, which they rarely used, and this hammock was only used once throughout the data collection period. This suggests that the red ruffed lemurs may not have used their hammock because it was located on the left side of their enclosure, which they rarely used. While the red ruffed lemurs may have their own individual preference not to use the hammock, it would be informative to reposition under-utilized environmental stimuli to determine if patterns of use are driven by the stimulus or by the position within the enclosure.

There is evidence from captive Alaotran gentle lemurs (*Hapalemur alaotrensis*) that the location of food may particularly influence what substrates lemurs choose to utilize, as well as their spatial use (Martin, Price, & Wormell, 2018). Alaotran gentle lemurs, who are primarily arboreal in the wild, will spend the majority of their time in the location where most of the growing vegetation is. Despite the presence of vertical poles and other substrates that would allow the lemurs to spend time at greater heights, they will choose to spend around 75.0% of their time on the ground (Martin et al., 2018). In the current study, the ring-tailed lemurs only used the hammock on the right side of their enclosure when the keeper placed food on it. A simple way to encourage increased usage of enclosure space would be to place highly desirable food items in differing sections of the enclosures. During data collection for the current study, keepers primarily limited food and foraging items to the half of the enclosure that each species used most often.

Some substrate use may appear limited because it was used for locomotion, such as the ropes and the bamboo bridge. Ring-tailed lemurs may have used the duck box so little simply because the box is heated and data collection occurred during the summer. They may use the duck box more frequently during colder months; a possibility supported by the finding that they were only observed using the duck box on a rainy day with a slightly lower temperature than usual. The low rates of substrate use for some objects do not necessarily mean that those objects are not important for the lemurs. In fact, given how the red ruffed lemurs tried to avoid directly moving on the ground, these objects appear to be a significant method of movement around the enclosure. Captive chimpanzees and gorillas will sit next to and climb on mesh at high rates in less natural enclosures but do so at very low rates in natural ones (Ross et al., 2009). Most of the substrates found in the lemur enclosures at the Woodland Park Zoo are naturally found in the lemurs' wild environment and, if they were artificial, such as the bamboo bridges that connected trees, they were made from natural materials. The hammocks were the only truly artificial substrate in that hammocks are not found in wild lemurs' environments, nor were the zoo hammocks made of materials found in their wild environment. But the hammocks did provide a large surface that enabled the lemurs to rest while off the ground. As depicted in Table 3, both species utilized all substrates available to them. The wide diversity of substrates in their enclosures as well as the natural characteristics of those substrates offer clear benefits to the lemurs. Each substrate offered some type of function, such as locomotion, resting, scanning the environment, or other behaviors.

Activity Budget

Both species in this study performed the highest proportion of behaviors engaged in inactive behaviors. Captive animals are typically less active than their wild counterparts, though this varies by zoo. This can lead to an increase in stereotypic behavior, aggression, and health issues, which can be especially significant for both captive ring-tailed and ruffed lemurs who are prone to obesity (Dye, 2017; Maloney, Meiers, White, & Romano, 2006; Schwitzer & Kaumanns, 2001). These levels of inactivity are often why environmental enrichment is so important for captive animals, as it promotes active engagement and can allow animals to deal with boredom or stress while engaging in their natural behaviors and can decrease the frequency of stereotypic behaviors (Maloney et al., 2006; Shyne, 2006). Furthermore, it is important to vary enrichment items routinely; captive animals, including lemurs, tend to habituate to enrichment objects, negating their benefits (Maloney et al., 2006).

Shire (2012) found that inactivity ranged from 53-67% of captive ring-tailed lemurs' activity budgets depending on the zoo. In the wild, ring-tailed lemurs spend 50-

55% of their time inactive (Jolly, 1966). As I only collected data during visitor hours during the day, and my data are in frequencies, rather than time, it is difficult to compare inactivity levels to that of wild populations. While the proportion of inactivity found in this study at the Woodland Park Zoo is lower than that found in the wild by Jolly (1966), this is likely because it does not include any data after 4:30pm. Inactivity is also lower than Shire's (2012) data. In part, this is likely due to differences in analysis; Shire (2012) considered autogrooming and allogrooming as inactive behaviors, whereas this study classified autogrooming as a miscellaneous behavior and allogrooming as a social behavior, as any form of grooming involves active engagement.

Data from wild populations at two different reserves in Madagascar indicate that wild ring-tailed lemurs spend 25-31% of their time foraging and 13-19% of their time traveling (Jolly, 1966; Keith-Lucas, White, Keith-Lucas, & Vick, 1999). The proportion of behaviors occupied by foraging and feeding in this study was much lower than in the wild, as expected. This is because captive animals are generally living in a much smaller area and, thus, do not have to travel very far for their food or resting places; furthermore, food is readily provided to them in the form of fruits, vegetables, and primate chow (Britt, 1998). The red ruffed lemurs did perform a similar proportion of behaviors locomoting, although the distance they traveled was obviously not very significant. Most of the movement from red ruffed lemurs consisted of vertical climbing and leaping to travel to higher or lower parts of the largest tree in their enclosure. As both species only utilized approximately half of their enclosure for the vast majority of behaviors, locomotion and, therefore, activity levels could be increased if lemurs were encouraged to use the rest of their enclosures.

Placing food in different parts of enclosures as well as on different substrates has been reported to increase feeding time, feeding enrichment interactions, as well as distance traveled to get food for captive black and white ruffed lemurs, thus decreasing inactivity (Kerridge, 2005). The ring-tailed lemur enclosure at the Woodland Park Zoo had one feeding enrichment device on the left side of the enclosure, where the animals performed most of their behaviors. Lemurs were observed occasionally utilizing this device. The red ruffed lemur enclosure did not have any feeding enrichment device visible. Meals served in the outdoor enclosures during visitor hours for both species consisted of the keeper placing food on the ground on the side of the enclosure the lemurs were already in, as well as hand-feeding some pieces to each lemur. While this is important, as it ensures each lemur is getting food, Maloney et al. (2006) found that captive ring-tailed and black lemurs preferred to actively work for their food in enrichment devices even when there was food available to them that they did not have to work for. This pattern has also been observed in captive small cats (Shepherdson, Carlstead, Mellen, & Seidensticker, 1993), macaques (Bryant, Rupniak, & Iversen, 1988), and otters (Foster-Turley & Markowitz, 1982). Increasing the number of strategically placed foraging devices in the enclosures could benefit lemurs by both increasing their activity and encouraging them to use more of their space. Even simply making food less visible to the lemurs can increase activity levels and time spent feeding and foraging (Dishman et al., 2009).

It is necessary to consider the behavioral ecology of each species independently. Simply moving food from the ground to trees may not increase activity levels of ring-tailed lemurs, who are semi-terrestrial (Britt, 1998; Jolly, 1966). However, suspending fruit from trees significantly increases activity levels for black and white ruffed lemurs, who are arboreal (Kerridge, 2005; Vasey, 2006), and also increases the amount of time they spend in the trees (Maloney et al., 2006). Red ruffed lemurs in this study performed more behaviors on the ground than they would in the wild, so it may be beneficial to provide suspended foraging devices. Placing species-appropriate devices in sections of the enclosures the lemurs do not utilize often would increase foraging time, increase activity levels as lemurs would have to travel more, and promote increased use of enclosure space.

Vigilance. Vigilance occupied an unexpectedly large portion of the activity budget, especially for ring-tailed lemurs. Vigilance is an important behavior for many species in the wild, such as birds, ungulates, and most other mammals, including primates. One of the primary reasons for vigilance is predator detection (Hunter & Skinner, 1998), and primates are more vigilant when predation risk is high (Steenbeek, Piek, van Buul, & van Hooff, 1999). In addition to predator detection, vigilance may help an individual avoid competition with conspecifics or simply provide awareness of the group's movements to keep connected (Dunbar, Cornah, Daly, & Bowyer, 2002). There is also direct evidence from primates that indicates that vigilance serves to monitor dominant conspecifics as well as coalition and mating partners (Baldellou & Henzi, 1992). In langurs (*Presbytis thomasi*), vigilance is connected to infanticide risks, as females with infants show the highest vigilance rates when near rival social groups (Steenbeek et al., 1999).

The ring-tailed lemur group in this study consisted of related males, so it is unlikely that their frequently observed vigilance was related to mating or coalition partners. Although agonistic encounters between the ring-tailed lemurs were only witnessed twice during data collection, zookeepers did state that there was a dominance hierarchy within the group. Therefore, some of the observed vigilance likely functioned to monitor conspecific behavior. However, given that most vigilance was not overtly directed at other lemurs, this does not seem to be the primary purpose here.

The “many-eyes effect” predicts that as the size of a group increases, the amount of time each individual has to spend being vigilant decreases (Powell, 1974). However, the larger group of ring-tailed lemurs in this study were more frequently vigilant toward all sources except for zoo visitors than were the smaller group of red ruffed lemurs. This included vigilance toward the sky, which often appeared to be in response to the sound of planes. Both species were most frequently vigilant towards unknown sources because the observer could not specifically identify environmental sounds that occurred in conjunction with vigilance behavior. While many sounds were likely construction and traffic noises due to the urban location of the zoo, the source of the noise could not be directly identified by the observer and, therefore, were classified as unknown.

As the presumed primary function of vigilance, predator detection is a likely explanation for some of the vigilance behavior observed in this study. Both ring-tailed lemurs and red ruffed lemurs respond to raptor calls, including in captivity (Macedonia & Yount, 1991), and though no raptors were witnessed in the area during this study, the lemurs were often vigilant toward birds in the area, including ducks, crows, and occasionally geese. If an aerial predator silhouette is similar enough to a raptor such as a hawk that ring-tailed lemurs encounter in the wild, they will give off alarm calls, even if the silhouette is small (Polak & Macedonia, 1989). It is considered species-typical behavior for lemurs to direct vigilance towards potential aerial predators. However, lemurs were also often vigilant toward overhead planes in the current study. Although cloud cover usually prevented planes from being seen from the ground, plane traffic could clearly be heard from the zoo.

Seattle-Tacoma International Airport, located approximately 17 miles from the zoo, is the eighth busiest airport in the United States. Data from several different locations across the Seattle-Tacoma area indicated that the average noise level from the airport from July to September in 2018 was 80.9dbA, which is a noise level measurement that takes into account how the human ear hears sounds (portseattle.org). Although data on noise levels for 2019 were not available, the airport's own data indicated that 2019 was busier in terms of passenger and flight numbers than was 2018. Data from rainforests indicate that noise levels are usually 27-40 dB, and two urban zoos similar to the Woodland Park Zoo were found to have average noise levels of 70 dB (Waser & Brown, 1986). While noise levels were not collected for this study, it is clear from extrapolation of the above data that the average noise level was likely much higher than the 27-40 dB range that lemurs would experience in the wild.

It is difficult to discern why the ring-tailed lemurs may have been more vigilant than the red ruffed lemurs in this study when the noise levels should have been equally bothersome to both species. With such a small sample size, individual differences in responsiveness to environmental stimuli could have skewed the results; the three red ruffed lemurs at the Woodland Park Zoo may have simply been less prone to vigilance than the average lemur. It is an interesting and unexpected finding, especially given that the red ruffed lemurs had an added reason to be vigilant—their social group contained a female of breeding age, and vigilance in primates has been linked to mate guarding as well as searching for mates (Dunbar et al., 2002). Because animal behavioral data were collected from July to September, the female would not have been in estrus and able to reproduce. Nevertheless, zookeepers stated that copulations did occasionally occur during this time period. Given the smaller group size of the red ruffed lemurs as well as the presence of potential mating opportunities, it is very surprising that the red ruffed lemurs were the less vigilant species.

If ring-tailed lemurs in the wild were killed by predators at a higher rate than red ruffed lemurs, ring-tailed lemurs would likely have evolved to be more vigilant. Karpanty (2005) estimated predation rates on black and white ruffed lemurs at one site to be approximately 4%, one of the lower rates in the area. Unfortunately, there are not published data estimating predation rates for red ruffed lemurs, who are limited to a much smaller range and are not sympatric with black and white ruffed lemurs (Tattersall, 1982). In addition, despite many examples of individual predation events on ring-tailed lemurs (e.g., Goodman, O'Connor, & Langrand, 1993; Karpanty & Wright, 2007), as well as a multitude of research on ring-tailed lemur antipredator behavior and calls (e.g., Bolt, Sauther, Cuozzo, & Youssouf, 2015; Gould, 1996; Gould & Sauther, 2007; Sauther, 1989), I was unable to find a specific predation rate or any comparison of ring-tailed and red ruffed lemur predation. While it cannot be discounted that ring-tailed lemurs may have evolved to be more vigilant than red ruffed lemurs due to increased predation risk, there is not enough data from wild populations to determine this.

When exposed to construction noises, captive giraffes, emus, and elephants all move to areas of their enclosures with less noise, and giraffes and elephants both increase their vigilance behaviors (Jakob-Hoff et al., 2019). Both lemur enclosures at the Woodland Park Zoo contained waterfalls to help reduce external noise. The waterfall in the ring-tailed lemur enclosure was located on the side that the ring-tailed lemurs rarely used, while the waterfall in the red ruffed lemur enclosure was located on the side that the red ruffed lemurs primarily used. It is possible that the waterfall does indeed help mitigate some sound, as it was meant to, and because the ring-tailed lemurs did not commonly utilize that side of their enclosure during the study period, they did not receive the intended noise-masking benefits of the waterfall feature. Therefore, they were more prone to being disturbed by external noises (e.g., planes, visitors, and construction) and had to devote more of their time to vigilance than the red ruffed lemurs. Research recording noise levels on both sides of the enclosure would be needed to determine whether this supposition is supported by actual noise level differences in the enclosure. In addition, foliage in the red ruffed lemur enclosure was visibly much denser than that in the ring-tailed lemurs' enclosure. Squirrel monkeys exhibit vigilance at higher rates when in open habitats with less canopy cover than when in habitats with more canopy cover (Boinski, 2003). The increased canopy cover could have allowed the red ruffed lemurs to feel more protected from aerial attacks and, thus, less inclined to dedicate time and energy to vigilance to the degree that ring-tailed lemurs did. Noise in open forests also tends to travel more than in dense forests (Marten & Marler, 1977), so in addition to or instead of the waterfall, the denser foliage cover in the red ruffed lemur enclosure may have minimized environmental noise stimuli that the ring-tailed lemurs were experiencing.

Unfortunately, there are no data from wild populations to determine whether the frequency of vigilance observed in the current study is comparable to that of wild lemurs. However, given that over 20% of the ring-tailed lemurs' observed discrete behaviors consisted of vigilance behaviors and previous research indicates that noise levels influence captive animals' behavior (Jakob-Hoff et al., 2019), it would appear that the amount of vigilance observed here may be excessive, suggesting that external noise at the zoo is consistently louder than what a wild lemur would experience and that it is difficult for captive animals to habituate to that noise. With the urban location of the zoo, decreasing environmental noise levels from construction, traffic, and planes is not feasible. However, designing at least a part of the enclosure to mitigate lemur's exposure to external noise—and better ensuring that the lemurs utilize that section of the enclosure—may be beneficial in allowing the lemurs to participate in other behaviors, such as foraging and locomotion, that are species-typical behaviors observed to be a large part of wild animals' repertoire.

Conclusions

Both the ring-tailed and red ruffed lemurs at the Woodland Park Zoo have complex naturalistic outdoor enclosures. Neither ring-tailed nor red ruffed lemurs appear to exhibit stereotypic behaviors or increased aggression levels, and to some extent, they utilize all substrates available to them, including but not limited to hammocks, rocks, ropes, and trees. Like many captive mammals, they dedicate a lower proportion of recorded behaviors to foraging and feeding than their wild counterparts. While it is difficult to compare captive and wild levels of inactivity, the frequencies of foraging and feeding observed in this study were quite low and could be increased by providing species-appropriate foraging devices and/or by spacing food delivery throughout more of their enclosures. In addition, although captive lemurs have limited space available to them, they do not utilize all of that space. It is possible that this specific set of lemurs was uncomfortable or wary of the other species and, therefore, avoided the section of their enclosure closest to the other species. In order to allow lemurs to utilize the full space available to them, it may be beneficial, in some contexts, to have more of a barrier between species that are unfamiliar with one another.

Lemurs in this study, especially ring-tailed lemurs, appeared to be excessively vigilant. The urban environment of the zoo is much louder than what lemurs in the wild would naturally experience, and given the high frequency of vigilance, the noise does seem to impact the lemurs. While noise mitigation techniques were incorporated into the enclosure design in the form of waterfalls, which may indeed function to reduce noise, this is not helpful if the lemurs are not utilizing areas near the waterfalls. I would expect that the noise levels experienced by the lemurs would be causing them stress; however, further research is needed to determine this.

Future Directions

More research is needed to determine whether the levels of vigilance observed here are consistent with levels of wild lemurs, or if the environmental stimuli around these lemurs at the zoo are truly disrupting their natural behavior patterns. I believe it is necessary to determine if there is a link between noise levels at a zoo such as the Woodland Park Zoo, which experiences many planes overhead each day and frequent construction, and resultant glucocorticoid levels in the zoo’s lemurs. Unfortunately, there is a lack of research on captive lemur species, despite their popularity in zoos. It may also be important to examine whether ring-tailed and red ruffed lemurs can comfortably live in mixed-species groups. Again, examining glucocorticoid levels would be a useful step in evaluating that possibility as would the frequency of aggression in connection with each species being alone or housed together.

Limitations

This study is limited by a small sample size. With only eight lemurs across two different species, it is difficult to generalize the trends observed here, especially since primates differ in individual behavioral traits, or personality (Freeman & Gosling, 2010). Furthermore, data were only collected at one zoo during one season. Behaviors and activity budgets often vary greatly from zoo to zoo (e.g., Shire, 2012; Webb et al., 2018), so to determine what may be successful at reducing noise requires additional data from other zoos; seasonality also significantly affects activity budgets for lemurs, with behavior being most affected during the breeding season (Jolly, 1966; Jolly, 1998), although the single female in this study was not in estrus at any point during data collection. It is also important to note that, given the distance between the observer and the lemurs, even while utilizing binoculars, it is possible that lemurs during some scans were misidentified, leading to some individuals being under or overrepresented in the data.

Despite these limitations, these data are still valuable for a multitude of reasons. Many zoos are located in urban areas, and as discussed, there is evidence to suggest that noise and stress levels are linked in captive mammals. These data indicate that captive lemurs are very attentive to noise and movement, whether it is from planes, visitors, construction, birds, or other external noises they would not experience in the wild. It is, therefore, important to know whether certain methods incorporated into enclosure design, such as the waterfalls at the Woodland Park Zoo, are appropriate methods to help reduce external noise and, therefore, reduce stress animals may experience. Furthermore, these data add to the existing literature demonstrating that captive primates spend less time foraging, feeding, and traveling than their wild counterparts and spend more time inactive and provides specific suggestions for increasing foraging and feeding time while also encouraging greater spatial use, which would therefore increase movement time. The lemurs at the Woodland Park Zoo did not demonstrate the typical signs of stress in captive mammals, such as overgrooming, increased aggression, or other stereotypic behaviors. They also did not appear to be severely impacted by levels of inactivity in terms of their visible well-being. However, the current findings underscore areas of lemur research that are lacking and suggest that noise levels in and around zoos, especially those in urban environments, may be affecting the behavior of captive lemurs.

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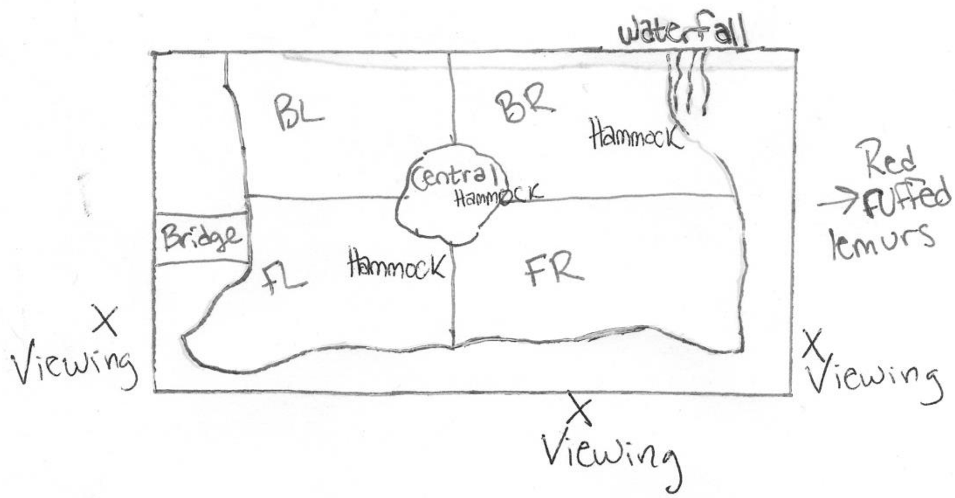
APPENDIX A

Lemur Exhibits and Viewing Areas

Ring-tailed lemur exhibit with viewing areas at the Woodland Park Zoo.



Red ruffed lemur exhibit with viewing areas at the Woodland Park Zoo.