Linköping University | Department of Physics, Chemistry and Biology
Type of thesis, 60 hp | Educational Program: Master's degree in Applied Ethology and Animal Biology
May 2020-May 2021 | LITH-IFM-A-EX-21/3967-SE

I like to move (it)

Use of outdoor space in a mixed exhibit of ring-tailed lemurs (*Lemur catta*) and red ruffed lemurs (*Varecia rubra*) at Furuvik Zoo

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1. Abstract

By studying how captive animals use outdoor space, we can determine which areas fulfill their biological and behavioral needs to improve enclosure design for animal welfare and visitor experience. The aim of the study was to determine the differential use of outdoor space in a mixed exhibit of captive ring-tailed lemurs (*Lemur catta*) and red ruffed lemurs (*Varecia rubra*), and to assess both the effect of adding environmental enrichment and possible visitor and meteorological effects on the lemurs' use of space and behavior. For one month, five-minute interval scan sampling was used to record lemur location and behavior, as well as the meteorological conditions and presence of zoo visitors in the lemurs' outdoor enclosure. That baseline was followed by four alternating two-week periods of food or structural enrichment, both with and without visitors. Enrichment increased the lemurs' use of the enriched sectors, decreased resting, and increased locomotion. Structural enrichment increased their exploratory behaviors and stimulated arboreal locomotion. Both species preferred sunny and warm conditions for sunbathing and resting, while moving more around the enclosure in cooler and cloudier weather. The visitor effect on the lemurs' use of space was weaker than the effects of enrichment and meteorological conditions. The availability of areas to hide and possible habituation to humans may have played a role in the reduced visitor effect. The results of the study showed inter-specific differences in the lemurs' use of space and behavior and a complex combined effect of enrichment, visitor presence and meteorological conditions.

2. Introduction

2.1. Captive animals' use of space

The way an animal uses space reflects its preferences based on its biological and behavioral needs (Goff et al., 1994; Stoinski et al., 2001; Ross et al., 2009). By studying how captive animals use outdoor space, we can learn how zoo enclosure areas are overutilized and underutilized, which, in turn, gives us an idea of how appropriate captive animals' environments are for them (e.g., Goff et al., 1994; Kessel and Brent, 1996; Ross et al., 2009). The information obtained from such studies can help improve enclosure design, therefore maximizing the animals' welfare while enriching the visitors' experience (Ross et al., 2011). However, there is still little conclusive information on how captive primates, especially lemurs, use outdoor enclosures in zoo environments (Ross et al., 2011) because only a few studies concerning use of space have been performed on lemurs (e.g., Macedonia, 1987; Hedge, 2005; Castiglioni et al., 2019).

Animals in the wild live in complex environments where they can move both horizontally and vertically. Primates exhibit a natural use of the vertical dimension (Mason, 1968), and therefore, both the horizontal and vertical size, complexity, and naturalism of captive environments are essential features for stimulating species-specific behaviors, including behaviors directly related to how the animals use space (e.g., Maple and Finlay, 1989; Perkins, 1992; Hebert and Bard, 2000).

2.2. Environmental enrichment to encourage natural behavior

One way to increase complexity is through environmental enrichment, defined by Newberry (1995) as a modification in the surrounding environment that improves the biological functioning of captive animals. Environmental enrichment can increase both an animal's choices and control over its environment (e.g., Maple and Finlay, 1989; Sambrook and Buchanan-Smith, 1997; Watters, 2009) as well as encourage species-specific behaviors, thus increasing the captive animal's physical and psychological well-being (Newberry, 1995; Shepherdson, 1998; Mellen and Sevenich MacPhee, 2001). Some benefits of environmental enrichment include increased ability to cope with stress in captivity, decreased stereotypical behaviors, and improved relationships with both familiar (caretakers) and unfamiliar (visitors) humans (e.g., Shepherdson, 1998; Mellen and Sevenich MacPhee, 2001; Carlstead, 1996).

Environmental enrichment has been subdivided into the categories of social (exposure to conspecifics), nutritional (food-related enrichment), physical (enclosure size and complexity, including permanent and temporary structures), occupational (interactive devices such as toys), and sensory (related to the five senses) enrichment (Bloomsmith et al., 1991; Young, 2003). Among these, it has been suggested that social enrichment best promotes species-specific behaviors and reduces stereotypies (Lutz and Novak, 2005). Although it is still unclear which type of enrichment is the most successful in zoos (Swaisgood and Shepherdson, 2005), studies carried out in primates, including lemurs, also consider nutritional and physical enrichment as some of the most effective ways to enhance captive environments (Schapiro and Blommsmith, 1995; Hedge, 2005). Enrichment should be selected based on the animal's behavior both in captivity and in the wild (Newberry, 1995; Mellen and Sevenich MacPhee, 2001; Lutz and Novak, 2005).

2.3. Food enrichment (nutritional)

In the wild, primates spend a significant proportion of their time foraging and feeding (Maple and Finlay, 1989; Lutz and Novak, 2005), which means that food enrichment should be a successful way to encourage those natural explorative and manipulative behaviors (e.g., Zimmermann and Feistner, 1996; Kerridge, 2005; Maloney et al., 2006), as well as other species-specific behaviors such as locomotion, playing and grooming (e.g., Maloney et al., 2006, Shapiro et al., 2018). One advantage of food enrichment is that it causes less habituation than other kinds of enrichment (Costa et al., 2018). However, only a few studies have focused on food enrichment in lemurs (e.g., Zimmermann and Feistner, 1996; Maloney et al., 2006; Shapiro et al., 2018). Some of the enrichment studies suggest the use of novel food items and foraging devices that make the animals work for their food, e.g., foraging balls, food puzzles and artificial feeders that can be hung on trees to encourage arboreal behaviors (e.g., Zimmermann and Feistner, 1996; Kerridge, 2005; Maloney et al., 2006).

2.4. Structural enrichment (physical)

Whenever possible, animals will use all the enclosure space available to them, mimicking their behavior in the wild (Hedge, 2005). Thus, behaviors such as exploration, locomotion and play can be positively affected by physical enrichment (e.g., Schapiro and Bloomsmith, 1995; Soriano et al., 2006; Sha et al., 2015). Some authors have suggested that the complexity and quality of structures present in an enclosure might be much more important than the size of

the enclosure itself (e.g., Wilson, 1982; Perkins, 1992; Stoinski et al., 2001). These structures could be either natural (trees, rocks, and water) or artificial (platforms, perches, ropes, swings, hammocks, nesting boxes, and foraging devices) (e.g., Wilson, 1982; Schapiro and Bloomsmith, 1995; Hedge, 2005). Although many studies reported on physical enrichment for captive animals, there are virtually none specifically on lemurs (Hedge, 2005).

2.5. Visitor effect on captive animals

The presence of zoo visitors has also been shown to have an effect on the behavior of captive animals, usually referred to as the "visitor effect" (e.g., Chamove et al., 1988; Hosey, 2000; Sherwen and Hemsworth, 2019). A few studies found that visitors have either no clear effect on the animals, probably because they are habituated to the presence of humans (Hosey, 2005; Collins et al., 2017; Goodenough et al., 2019), or that they have a positive effect, especially if there is food involved (Cook and Hosey, 1995). However, most studies concluded that visitors have a negative impact (e.g., Wood, 1998; Mallapur et al., 2005; Quadros et al, 2014), including a few studies in lemurs (e.g., Hosey and Druck, 1987; Chamove et al., 1988). Large, active, noisy crowds seem to be the most stressful for captive primates (Hosey and Druck, 1987; Hosey, 2000), and this visitor effect is particularly marked in small diurnal arboreal species (Chamove et al., 1988; Queiroz and Young, 2018). Moreover, some studies suggest an interaction between environmental enrichment and visitor effects (Wood, 1998), while others indicate an interaction between visitor effects and use of space (Hosey and Druck, 1987; Mitchell et al, 1992; Mallapur et al., 2005).

2.6. Effect of meteorological conditions on captive animals

Together with time of day and season, meteorological conditions have been shown to have an important effect on visitor numbers and on animal behavior and their use of space (e.g., Collins et al., 2017; Goodenough et al., 2019). When considering meteorological conditions, most studies have focused on weather as an umbrella of parameters that includes various gradients of cloud coverage, sun, and precipitation, together with other aspects such as temperature and humidity (e.g., Collins et al., 2017). However, very few studies have analyzed temperature as a separate parameter that might affect animals differently from other meteorological factors (Vasey, 2005).

2.7. Lemurs

Lemurs are prosimians belonging to the suborder Strepsirrhini, a group of non-human primates (Yoder, 2007). In the wild, they are endemic to the island of Madagascar (Mittermeier et al., 1994; Yoder, 2007). They constitute more than 15% of living primate species, though they occur on less than 0.4% of Earth's land surface area (Yoder, 2007).

While lemurs are considered less curious and slower at learning than other primates (Sauther et al., 1999), they are inquisitive about novel objects (Jolly, 1964). However, they have limited object manipulation capabilities (Jolly, 1964; Kappeler, 1987; Sauther et al., 1999).

Ring-tailed lemurs and red ruffed lemurs are in the same family, Lemuridae. They share many traits, but there are some important morphological and behavioral differences (Hedge, 2005).

2.7.1. Ring-tailed lemurs

The ring-tailed lemur (*Lemur catta*) is the most common lemur in captivity (Mittermeier et al., 1992; Baker et al., 2017), and it is ranked as an endangered species in the IUCN Red List of Threatened Species. In the wild, they inhabit only the southern and southwestern portion of the island of Madagascar, where they live in a variety of habitats (Mittermeier et al., 1994).

This medium-sized, monomorphic species is female-dominant and exhibits relatively stable intra-group dominance hierarchies (Jolly, 1966; Sauther et al., 1999; Gould et al., 2003).

Ring-tailed lemurs are mostly considered a diurnal species (e.g., Jolly, 1966; Martin, 1972; Bray et al., 2017), although signs of cathemeral activity might exist in the wild during periods with high daytime temperatures (Donati et al., 2013). They rest almost 50% of their time, feed and forage around 25%, move and travel almost 20%, sunbathe around 5%, sleep 2% and groom 2% of their time (Sussman, 1977; Britt, 2000; Rasamimanana et al., 2006).

Unlike most lemurs, which are almost exclusively arboreal, semi-terrestrial ring-tailed lemurs use terrestrial locomotion for foraging and traveling 30% of the time on average (Sussman, 1977; Sauther et al., 1999). They may even spend up to 75% of their time on the ground depending on habitat and season, making them the most terrestrial living lemur (e.g., Jolly, 1966; Budnitz and Dainis, 1975; Sussman, 1977). However, they are still strong climbers and move through all forest strata (Mittermeier et al., 1994).

They are considered opportunistic omnivores (Sauther et al., 1999), although they mostly have a frugivorous/folivorous diet (60-90%) that they complement with bark, dead wood, sap, insects and soil (e.g., Jolly, 1966; Sussman, 1977; Rasamimanana and Rafidinarivo, 1993).

2.7.2. Red ruffed lemurs

The red ruffed lemur (*Variegata rubra*) is a critically endangered species on the IUCN Red List of Threatened Species whose habitat is restricted to the rainforest of the Masoala peninsula in northeastern Madagascar (Petter et al., 1977).

This female-dominant species (Macdonald, 1984) is the largest of the living lemurs (Britt, 2000; Vasey, 2005).

This diurnal-crepuscular species is more active at early morning and late afternoon (e.g., Petter, 1962; Martin, 1972; Kress et al, 1978), and they sleep for a large part of the day (Macdonald, 1984). They also like to sunbathe during the day. In captivity, signs of possible cathemerality have also been observed (Bray et al. 2017). They spend up to 53% of their time resting (Vasey, 2005), 22-28% feeding (Britt, 1998; Vasey, 2005) and 12-19% in locomotion (Britt, 2000; Vasey, 2005).

Red ruffed lemurs are considered arboreal quadrupeds (e.g., Martin, 1972; Pereira et al., 1988; Britt, 1998); however, they also exhibit vertical clinging and leaping at low levels in the forest (Pereira et al., 1988). Contrary to ring-tailed lemurs, they are rarely on the ground and spend most of their time in the upper canopy (Britt, 2000; Vasey, 2004). Suspensory postures account for 25% of their feeding postures (Britt, 2000).

Red ruffed lemurs are the most frugivorous of the living lemurs (Rigamonti, 1993; Vasey, 2004); fruit comprises 88-92% of their diet (Britt, 2000; Vasey, 2005), and they occasionally feed on fungi (Britt, 1998), leaves, flowers and nectar (e.g., Rigamonti, 1993; Britt, 2000; Vasey, 2004). Most feeding (75%) occurs at 10-25 m above the forest floor (Britt, 2000).

2.8. Aim of the study

To the best of my knowledge, no previous study has focused on both the horizontal and vertical use of outdoor space in a mixed exhibit of captive lemurs, analyzed together with the combined effect of enrichment, visitor presence and meteorological conditions.

Thus, the aim of this study was to determine the differential use of outdoor space by a mixed-species group of captive ring-tailed lemurs and red ruffed lemurs, as well as to assess the effect of enrichment, visitors, and meteorological conditions on that differential use of outdoor space. The final purpose was to generate knowledge that may help improve future enclosure design which, in turn, may enhance the lemurs' natural behaviors, thus improving their welfare and increasing educational value for the visitors.

3. Materials and methods

3.1. Study animals

Fig. 1. Ring-tailed lemurs (*Lemur catta*)


Fig. 2. Red ruffed lemurs (*Varecia rubra*)

This study was carried out on nine ring-tailed lemurs (Fig. 1) and two red ruffed lemurs (Fig. 2) housed in a mixed exhibit at Furuvik Zoo, Gävleborg, Sweden (see Appendix for specific information on each lemur).

All the ring-tailed lemurs were born at Furuvik Zoo except for the oldest male and female, who arrived at the zoo in 2005 and 2006, respectively. The two red ruffed lemurs came to Furuvik Zoo from other European zoos in 2017.

3.2. Enclosure


Fig. 3. The lemurs' outdoor area.

The lemurs' enclosure at Furuvik Zoo comprises an outdoor area of 5,000 m^2, within which two indoor enclosures are located: the ring-tailed lemurs' house (200 m^3) and the red ruffed lemurs' house (500 m^3). A few other human-made constructions can be found in the outdoor area: an information cabin, a wooden bridge, a couple of bamboo structures close to the red ruffed lemurs' house, and a wooden structure close to the ring-tailed lemurs' house. Moreover, a few bamboo poles connect the bamboo structures and the entrance of the red ruffed lemurs' house, while several ropes hang among multiple trees around the outdoor enclosure. Two outdoor gates and a path allow visitors to enter, walk around, and exit the lemurs' outdoor enclosure.

The enclosure's outdoor area is covered in vegetation, including trees, bushes, shrubs, and grass.

3.3. Data collection

Due to the size of the outdoor enclosure, I moved around the outdoor area to be able to locate every individual as I collected data. However, to avoid possible confounding effects, I stayed on the visitors' path as much as possible and kept a distance of 5-10 meters from the lemurs, moving slowly and quietly. Data were always collected using an interval timer on a mobile phone, Swift 8.5×44 binoculars, a stone paper notebook and a pen.

Due to the difficulty of quickly and accurately telling the individuals apart, I collected data at a group level. However, I was able to distinguish each lemur separately after the first two weeks of pilot study, so notes on individual behavior were also recorded during the subsequent baseline and enrichment studies.

A. Pilot study

During the last two weeks of June 2020, I carried out a 50-hour pilot study to test the sampling methods and confirm the adequacy of the study aims. During this pilot study, I collected data through 5-minute interval scan sampling (Altmann, 1974) to get a general idea of both species' initial use of space with and without the presence of visitors. Data recorded included the instantaneous location and behavior of all eleven individuals together with parameters such as meteorological conditions and presence of visitors in the lemurs' outdoor enclosure. Meteorological conditions were categorized by sky cover and rainfall into sunny (open sky, sun shining), cloudy (sky covered with clouds that hide the sun) or rainy

(precipitation), and those weather categories were further subdivided by temperature into cold (8-15ºC), mild (16-19ºC) and warm (20-30ºC) subcategories. I obtained the day's temperature from the website www.timeanddate.com and recorded it in the day's notes.

Using the data obtained during this pilot study, I divided the outdoor enclosure into ten sectors (A-J) (Fig. 4, see Appendix for more information on each sector) and four levels of height above ground (0-3) (Table 1) to be used for the subsequent baseline and enrichment studies.

Fig. 4. Map of the outdoor enclosure divided into ten sectors.

Table 1. Levels of height above ground in the outdoor enclosure.

Vertical location - Levels			
Ground (0-1 meters) (includes small rocks and trunks)	Low canopy (1-10 meters)	Middle canopy (10-20 meters)	High canopy (>20 meters)
0	1	2	3

Prior to the pilot study, I created a preliminary ethogram based on information collected from literature. During those two weeks, I collected data on the lemurs' behavior ad libitum (Martin and Bateson, 2007) in order to adapt the ethogram to the zoo's lemur population (Table 2). The animals also got used to my presence during this time.

Table 2. Ethogram of recorded behaviors.

Behavior	**Definition**
Resting	Inactive: sleeping, lying down, sunning, sitting, standing
Locomotion	Moving by walking, running, jumping, climbing
Feeding/foraging	Manipulation of food, eating, drinking
Interaction with conspecifics	Grooming, playing, fighting

B. Baseline study

Once the pilot study ended, the actual collection of observational data started. I collected data with the same 5-minute interval scan sampling method used for the pilot study (Altmann, 1974) during both the baseline and the enrichment studies. During July 2020, I conducted a 120-hour baseline study when the zoo was open to visitors and before enrichment was added to the enclosure. Data were collected for a total of 20 days with 6 hours of observation a day divided into morning and afternoon sessions taking place between 9:00 and 17:00. Once the baseline study was finished, the enrichment period started.

C. Enrichment study

The first two-week **food enrichment period** was carried out during the first half of August. I placed food enrichment devices on the sectors of the outdoor space that were used least by each species of lemur during the baseline study. The devices chosen were already familiar to the lemurs to avoid neophobia and lure the lemurs into the desired sectors (Fig. 5):

1) two closed wooden "problem boxes" with pieces of food hidden among hay (one with side holes and one without) (Fig. 5 A).
2) four plastic balls of different sizes and colors with holes and pieces of food among hay (Fig. 5 B).
3) one bottle spinner with small pieces of food (Fig. 5 C).
4) two long, black, metallic "bird feeders" with pieces of food hidden among hay (Fig. 5 D).
5) two non-lidded wooden crates with pieces of food hidden among hay (Fig. 5 E).
6) three metallic skewers with whole food (Fig. 5 F).

For the ring-tailed lemurs, the devices were placed at a height of approximately 1 meter above ground on two existing trunks in sector I. For the red ruffed lemurs, the devices were hung on ropes at a height of around 4-5 meters above ground in sector J. The only exception occurred on the first day of the study period, when the device for the red ruffed lemurs was placed in four different sectors (H, A, B, J); I positioned some of the additional devices close to their indoor enclosure to help the animals feel comfortable enough to venture away from that area. The hanging devices for the red ruffed lemurs were placed to encourage use of suspensory feeding postures. To avoid habituation and to assess the efficiency of various food enrichment alternatives, I rotated a combination of the six different available food enrichment devices with one device per species per day (Table 3). The food used in those enrichment devices consisted of their daily diet plus extra fruit and sweet vegetables as treats. The extra food

items were chosen from the lemurs' regular diet to avoid neophobia and to make sure that the nutrient composition of their diet followed their nutritional needs. To avoid continuous reinforcement, I replaced food at different intervals throughout the day.

During this first food enrichment period, the zoo was still open to visitors. This enrichment period spanned 60 hours over 12 days during which I collected data for 5 hours per day between 9:00 and 17:00.

Fig. 5. Food enrichment devices (A: problem box; B: plastic ball; C: bottle spinner; D: bird feeder; E: wooden crate; F: skewer)

Table 3. Rotational food enrichment device scheme.

	Ring-tailed lemurs		**Red ruffed lemurs**	
Days	***Device***	***Location***	***Device***	***Location***
1 Aug	Problem boxes	Sector I Level 0	Plastic balls	Sectors H, A, B, J Level 1
6 & 10 Aug 1, 6 & 11 Sep	Problem boxes	Sector I Level 0	Plastic balls	Sector J Level 1
2, 7 & 14 Aug 2, 7 & 13 Sep	Bottle spinner	Sector I Level 0	Bird feeders	Sector J Level 1
3, 8 & 15 Aug 3, 9 & 14 Sep	Wooden crates	Sector I Level 0	Wooden crates	Sector J Level 1
4, 9 & 16 Aug 5, 10 & 15 Sep	Bird feeders	Sector I Level 0	Skewers	Sector J Level 1

The first two-week **structural enrichment period** was carried out during the second half of August, when physical structures were redistributed around the enclosure and additional structures were added as described in Fig. 6 and Table 4. The goal of structural enrichment was to give the lemurs more opportunities to move around the enclosure and increase the use of areas that had been identified as neglected during the baseline study.

Fig. 6. Structural enrichment (A: horizontal bamboo structure; B: diagonal bamboo structure; C: bamboo poles and poplar trunk among trees; D: ropes among trees forming an aerial "highway")

Table 4. Scheme of structural enrichment.

	Ring-tailed lemurs		**Red ruffed lemurs**	
Days	***Device***	***Location***	***Device***	***Location***
17-18, 20-23, 25-26, 28-30 Aug	Horizontal bamboo structure on the ground	Sector I Level 0	Bamboo poles & poplar trunk among trees	Sector J Level 1 (6-7 m)
17-19, 21-23, 25-27, 29 Sep	Diagonal bamboo structure on the ground	Sectors E-F Levels 0-1	Ropes among trees (aerial "highway")	Sectors H-G-F Level 1 (6-8 m)

The same enrichment schedule was followed during the month of September, with two weeks of food enrichment followed by two weeks of structural enrichment. However, the zoo was closed to visitors in September. That month, I collected a total of 120 hours of data during the day between 9:00 and 16:00.

3.4. Data analysis

I divided the data from the baseline and enrichment periods into four main categories for analysis: outdoor presence, sectors, levels and behavior. I pooled the daily 5-min interval data points by category for each species, then added up those daily amounts into a total amount for the whole period (see Appendix).

I did the same pooling of data points by visitor presence and the meteorological conditions already described in the pilot study.

To determine how evenly data on the use of outdoor space were distributed, I calculated the spread of participation (SP) index (also known as SPI) (Dickens, 1955; Hedeen, 1983). The formula for the SPI is as follows:

SPI = [M (nb - na) + (Fa - Fb)] / 2 (N – M)

In this formula, N is the total number of data points in a category; M is the mean number of data points in all subcategories (N / number of subcategories); nb is the number of subcategories with fewer data points than M; na is the number of subcategories with more data points than M; Fa is the total number of data points in subcategories with more data points than M; and Fb is the total number of data points in subcategories with fewer data points than M. The SPI ranges from 0 to 1; the lower the number, the more evenly distributed the data is. An SPI between 0 and 0.2 indicates that data are evenly distributed, values between 0.3 and 0.8 indicate an uneven distribution, and an index of 1 indicates that all data are completely clustered in one single group or place.

I used the Shapiro-Wilk test to determine data normality. The data were not normally distributed, which led me to choose a non-parametric test. Because all study data were categorical, I chose the non-parametric chi-squared test (known as χ^2), calculated according to Preacher (2001).

I transformed the total amount of data points for each category and parameter in all study periods into percentages for statistical data analysis using the χ^2 test.

4. Results

4.1. Outdoor presence

4.1.1. Enrichment effect on lemurs' outdoor presence

The lemurs' outdoor presence subdivided by enrichment period is shown in Fig. 7. The ring-tailed lemurs were present outdoors significantly less during the structural enrichment period than during either the baseline ($\chi^2_{(1)} = 11.67$, $p < 0.01$) or the food enrichment period ($\chi^2_{(1)} = 6.61$, $p = 0.010$). In contrast, the red ruffed lemurs were present outdoors significantly more during the food enrichment period than either the baseline ($\chi^2_{(1)} = 4.39$, $p < 0.05$) or the structural enrichment period ($\chi^2_{(1)} = 11.32$, $p < 0.01$).

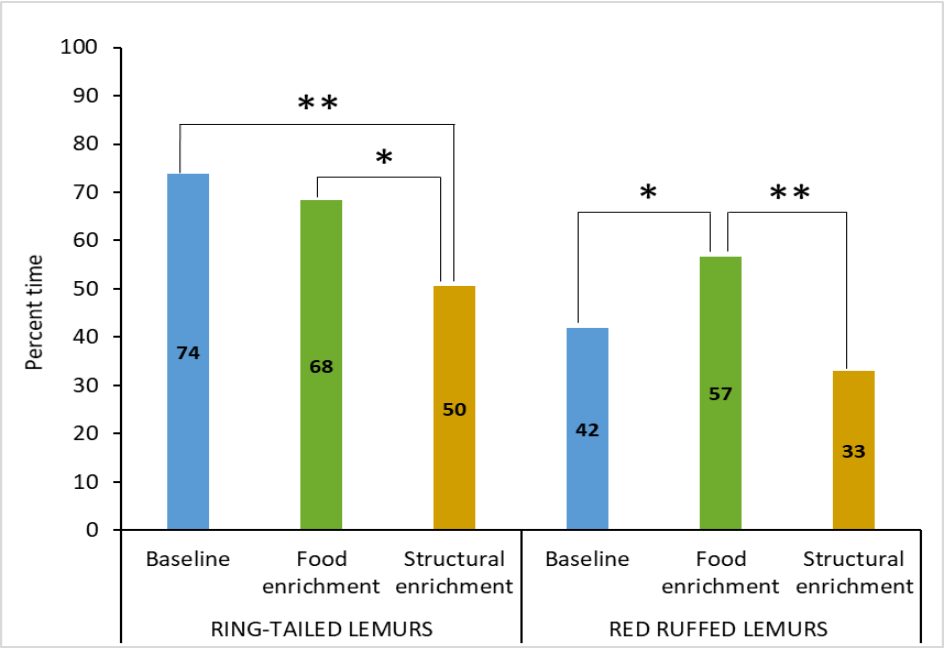

Fig. 7. Lemurs' outdoor presence subdivided by enrichment period.
* $p < 0.05$ (χ^2 test) / ** $p < 0.01$ (χ^2 test)

4.1.2. Visitor effect on lemurs' outdoor presence

The lemurs' outdoor presence subdivided by visitor presence is shown in Fig. 8. The ring-tailed lemurs were present outdoors significantly more with visitors than with no visitors ($\chi^2_{(1)} = 13.12$, $p < 0.01$). The same was true for the red ruffed lemurs, although their result was less significant than for the ring-tailed lemurs ($\chi^2_{(1)} = 4.25$, $p < 0.05$).

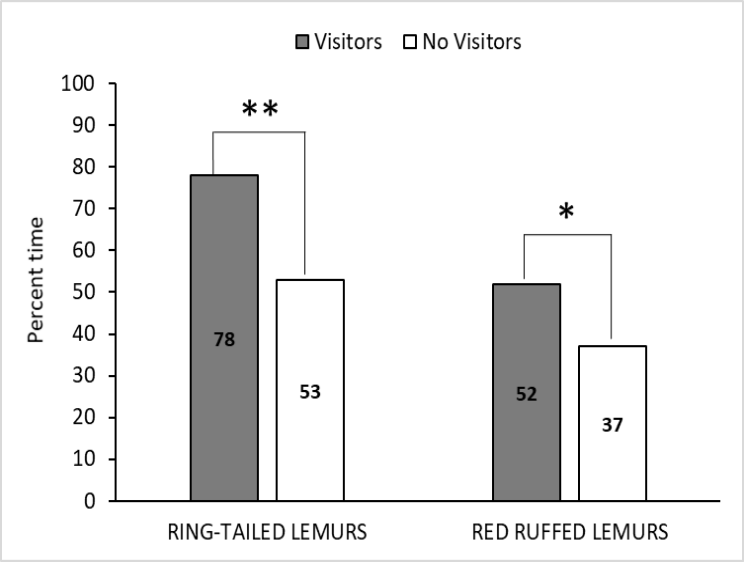

Fig. 8. Lemurs' outdoor presence subdivided by visitor presence.
* $p < 0.05$ / ** $p < 0.01$ (χ^2 test)

4.1.3. Weather effect on lemurs' outdoor presence

The lemurs' outdoor presence subdivided by weather is shown in Fig. 9. The ring-tailed lemurs were outdoors significantly more when it was sunny than either cloudy ($\chi^2_{(1)} = 19.18$, $p < 0.01$) or rainy ($\chi^2_{(1)} = 114.91$, $p < 0.01$). They were also outdoors significantly more in cloudy than rainy conditions ($\chi^2_{(1)} = 51.12$, $p < 0.01$). The red ruffed lemurs were outdoors significantly less when it was rainy than either sunny ($\chi^2_{(1)} = 9.12$, $p < 0.01$) or cloudy ($\chi^2_{(1)} = 4.14$, $p < 0.05$).

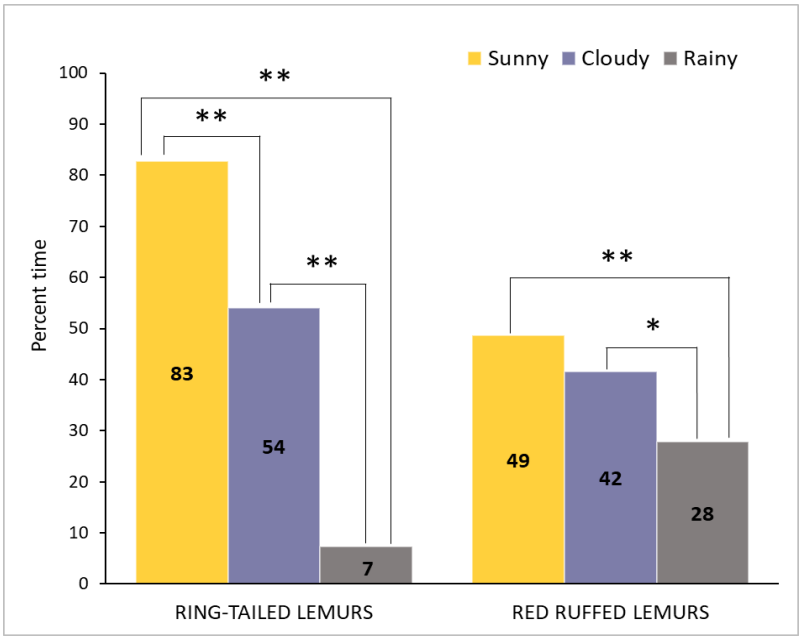

Fig. 9. Lemurs' outdoor presence subdivided by weather.
* $p < 0.05$ / ** $p < 0.01$ (χ^2 test)

4.1.4. Temperature effect on lemurs' outdoor presence

The lemurs' outdoor presence subdivided by temperature is shown in Fig. 10. The ring-tailed lemurs were outdoors significantly more when it was warm than in either mild ($\chi^2_{(1)} = 11.99$, $p < 0.01$) or cold ($\chi^2_{(1)} = 31.78$, $p < 0.01$) temperatures. They were also outdoors significantly more when temperatures were mild than cold ($\chi^2_{(1)} = 5.39$, $p = 0.020$). The red ruffed lemurs were outdoors significantly less in cold than either mild ($\chi^2_{(1)} = 3.89$, $p = 0.049$) or warm temperatures ($\chi^2_{(1)} = 11.61$, $p < 0.01$).

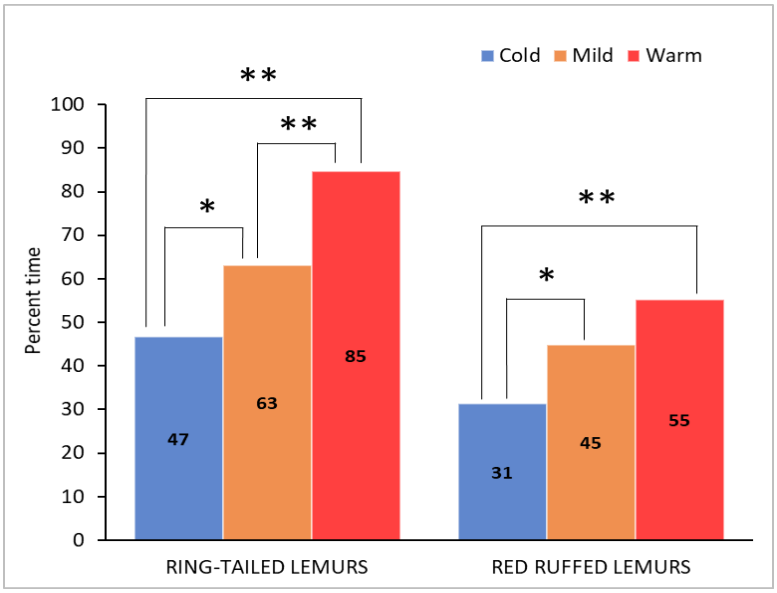

Fig. 10. Lemurs' outdoor presence subdivided by temperature.
* $p < 0.05$ / ** $p < 0.01$ (χ^2 test)

4.2. Use of sectors

4.2.1. Enrichment effect on lemurs' use of sectors

The lemurs' use of outdoor space subdivided by sector and enrichment period is shown in Fig. 11. The differences in the ring-tailed lemurs' use of space by sector were significant between the baseline and either the food enrichment period ($\chi^2_{(9)} = 25.39$, $p < 0.01$) or the structural enrichment period ($\chi^2_{(9)} = 31.01$, $p < 0.01$), but not between enrichment periods. The ring-tailed lemurs were in sector A (open area) significantly less but in sectors C (ring-tailed house) and I (enriched) significantly more during the food enrichment period than during the baseline. During the structural enrichment period, they used sectors A (open area) and I (enriched) less and sectors C (ring-tailed house) and B (open area) more than during the food enrichment period, although these differences were not statistically significant. However, the ring-tailed lemurs still used sector I (enriched) significantly more during the structural enrichment period than during the baseline. They used sector H (red ruffed house) the least during the food enrichment period. The ring-tailed lemurs used sector J (enriched) equally during either enrichment period but significantly more during those periods than the baseline.

The red ruffed lemurs' use of space by sector was significantly different between the baseline and either the food enrichment period ($\chi^2_{(9)} = 57.29$, $p < 0.01$) or the structural enrichment period ($\chi^2_{(9)} = 34.25$, $p < 0.01$). Moreover, the differences were also significant between

enrichment periods ($\chi^2_{(9)} = 25.07$, $p < 0.01$). The red ruffed lemurs used sector H (red ruffed house) significantly less and sector J (enriched) significantly more during the food enrichment period than during the baseline. They also used sector I (enriched) significantly more during the food enrichment period than during the baseline or structural enrichment period. During the structural enrichment period, the red ruffed lemurs used sector J (enriched) significantly less and sector H (red ruffed house) significantly more than during the food enrichment period, but neither sector's use returned to baseline levels. Sector D (treed area with cabin) was consistently the third-most-used sector overall and the most-used sector during the structural enrichment period.

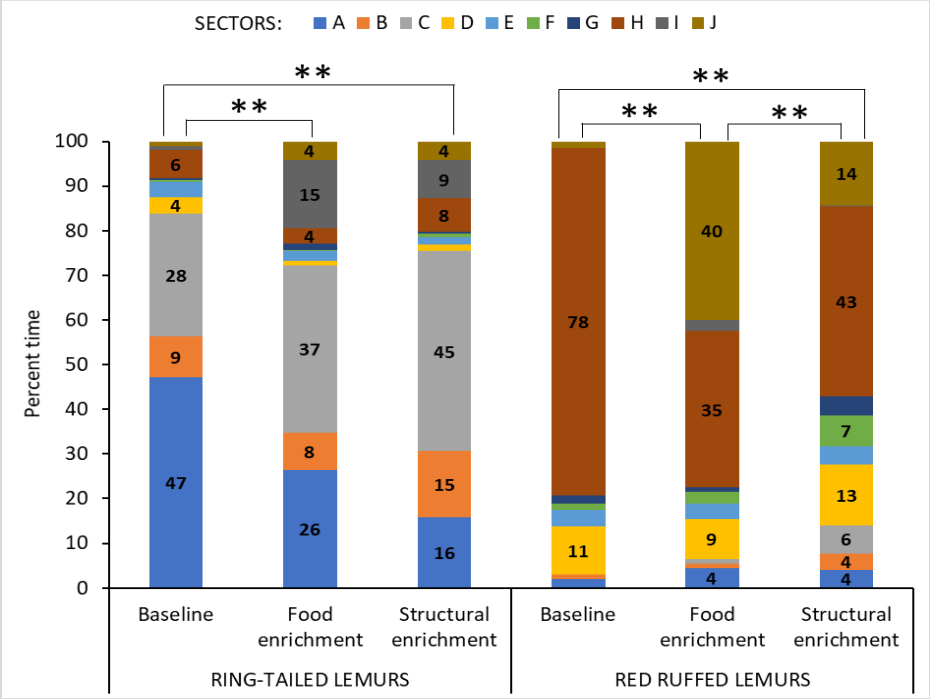

Fig. 11. Lemurs' use of outdoor space subdivided by sector and enrichment period.
** $p < 0.01$ (χ^2 test)

The lemurs' use of outdoor space by sector was never evenly distributed ($0.40 < SPI < 0.80$). However, the use of space tended to be more evenly distributed during the enrichment periods than during the baseline. The ring-tailed lemurs' SPI went from 0.61 during the baseline (94% of time spent in 5 sectors) to 0.55 during the food enrichment period (95% of time spent in 6 sectors) and finally to 0.50 during the structural enrichment period (96% of time spent in 6 sectors). The red ruffed lemurs' SPI went from 0.76 during the baseline (88% of time spent in 2 sectors) to 0.61 during the food enrichment period (88% of time spent in 4 sectors) and finally to 0.45 during the structural enrichment period (91% of time spent in 7 sectors).

4.2.2. Visitor effect on lemurs' use of sectors

The lemurs' use of outdoor space subdivided by sector and visitor presence is shown in Fig. 12. The differences between the ring-tailed lemurs' use of sectors with visitors and with no visitors were not statistically significant ($\chi^2_{(9)} = 10.08$, $p > 0.05$). However, the ring-tailed lemurs used sectors A (open area) and C (ring-tailed house) less and sectors B (open area), I and J (enriched), and H (red ruffed house) more with no visitors than with visitors.

The differences between the ring-tailed lemurs' use of sectors with visitors and with no visitors were significant ($\chi^2_{(9)} = 19.89$, $p = 0.019$). These differences were especially significant for sectors H, D and J ($\chi^2_{(2)} = 9.09$, $p < 0.01$). The red ruffed lemurs used sector H (red ruffed house) significantly less and sectors D (treed area with cabin) and J (enriched) significantly more with no visitors than with visitors.

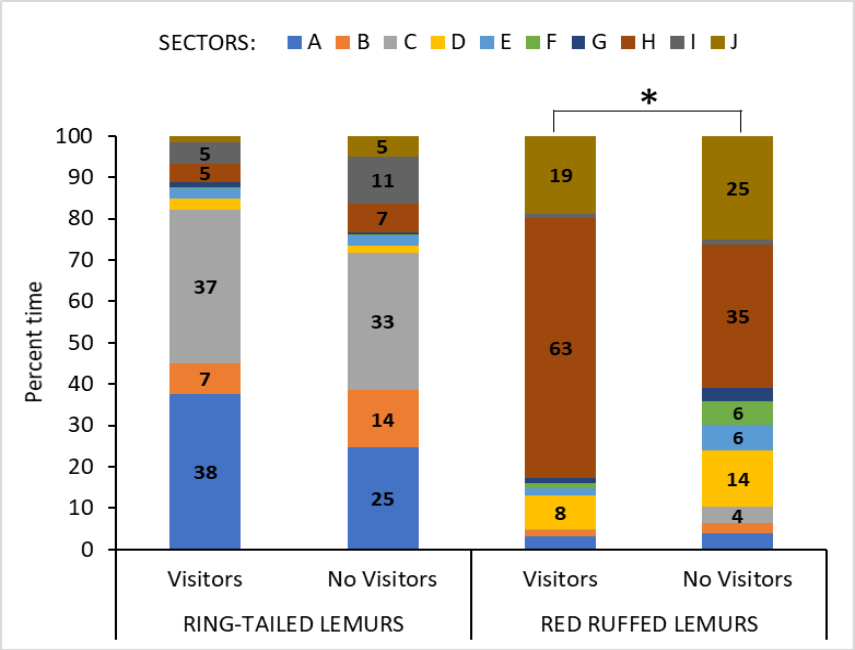

Fig. 12. Lemurs' use of outdoor space subdivided by sector and visitor presence.
* $p < 0.05$ (χ^2 test)

The lemurs' use of outdoor space by sector was never evenly distributed either with or without visitors ($0.45 < SPI < 0.70$). However, their use of sectors was more evenly distributed with no visitors than with visitors. The ring-tailed lemurs' SPI was 0.61 with visitors (92% of time spent in 5 sectors) and 0.48 with no visitors (95% of time spent in 6 sectors). The red ruffed lemurs' SPI was 0.68 with visitors (90% of time spent in 3 sectors) and 0.48 with no visitors (90% of time spent in 6 sectors).

4.2.3. Weather effect on lemurs' use of sectors

The lemurs' use of outdoor space subdivided by sector and weather is shown in Fig. 13. The differences in the ring-tailed lemurs' use of sectors were significant between rainy and either cloudy ($\chi^2_{(9)} = 35.19$, $p < 0.01$) or sunny conditions ($\chi^2_{(9)} = 51.44$, $p < 0.01$). The ring-tailed lemurs used sectors A and B (open areas) as well as enriched sector I the most in sunny weather and the least in rainy conditions. The opposite was true for sectors C (ring-tailed house), J (enriched), E (furthest treed area) and D (treed area with cabin). The ring-tailed lemurs used sector H (red ruffed house) the most in cloudy conditions.

Like the ring-tailed lemurs, the differences in the red ruffed lemurs' use of sectors were also significant between rainy and either cloudy ($\chi^2_{(9)} = 32.35$, $p < 0.01$) or sunny conditions ($\chi^2_{(9)} = 33.32$, $p < 0.01$). They used sector H (red ruffed house) the most in sunny weather and the least in rainy conditions. The opposite was true for sectors D (treed area with cabin), B (open area) and C (ring-tailed house). The red ruffed lemurs used sector J (enriched) the least in cloudy conditions.

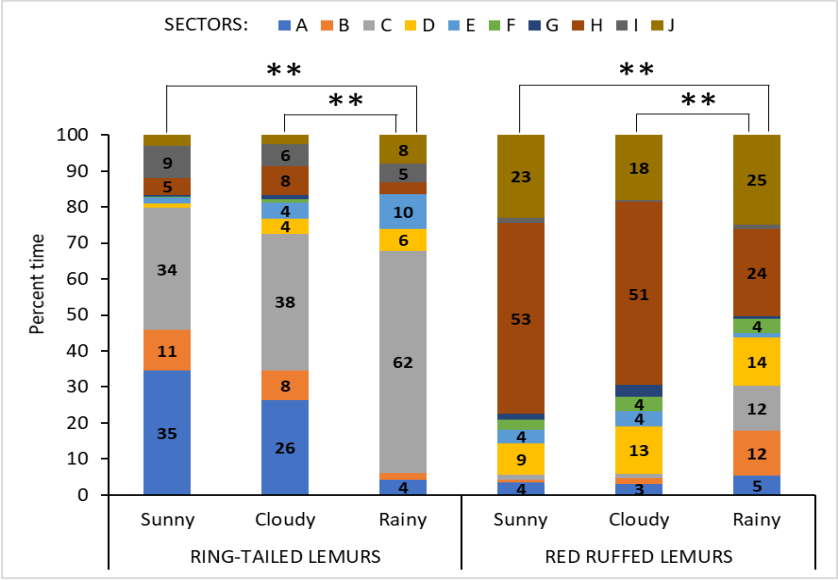

Fig. 13. Lemurs' use of outdoor space subdivided by sector and weather.
** $p < 0.01$ (χ^2 test)

The lemurs' use of outdoor space by sector was never evenly distributed among weather conditions ($0.40 < SPI < 0.65$). However, there were some species-specific differences. The ring-tailed lemurs' use of sectors was more evenly distributed in cloudy (SPI: 0.49, with 95% of time spent in 7 sectors) than in either sunny (SPI: 0.55, with 93% of time spent in 5 sectors) or rainy conditions (SPI: 0.57, with 95% of time spent in 6 sectors). The red ruffed lemurs' use of sectors was more evenly distributed in rainy (SPI: 0.42, with 97% of time spent

in 7 sectors) than in either cloudy (SPI: 0.58, with 94% of time spent in 6 sectors) or sunny conditions (SPI: 0.62, with 92% of time spent in 5 sectors).

4.2.4. Temperature effect on lemurs' use of sectors

The lemurs' use of outdoor space subdivided by sector and temperature is shown in Fig. 14. The differences in the ring-tailed lemurs' use of sectors were significant between warm and cold temperatures ($\chi^2_{(9)} = 17.78$, $p < 0.05$). These differences were especially significant for sectors A, B and C between warm and either cold ($\chi^2_{(2)} = 12.75$, $p < 0.01$) or mild temperatures ($\chi^2_{(2)} = 10.87$, $p < 0.01$). The ring-tailed lemurs used sector C (ring-tailed house) the most when it was warm and the least when it was cold. The opposite was true for sectors A and B (open areas).

Like the ring-tailed lemurs, the differences in the red ruffed lemurs' use of sectors were significant between cold and warm temperatures ($\chi^2_{(9)} = 19.34$, $p = 0.022$). The red ruffed lemurs used sectors H (red ruffed house) and J (enriched) the most when it was warm and the least when it was cold, while the opposite was true for sector D (treed area with cabin), sectors A and B (open areas), as well as sector C (ring-tailed house).

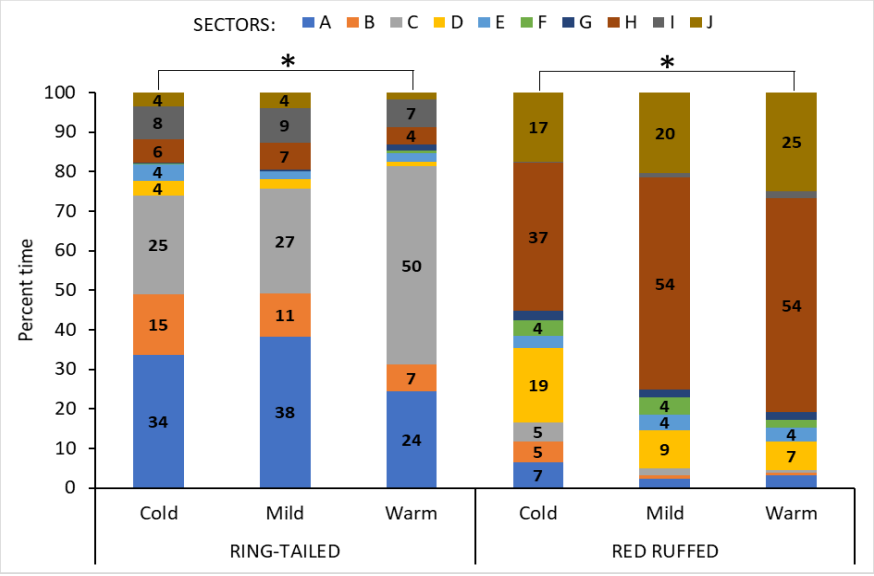

Fig. 14. Lemurs' use of outdoor space subdivided by sector and temperature.
* $p < 0.05$ (χ^2 test)

The lemurs' use of outdoor space by sector was never evenly distributed among temperature subcategories ($0.45 < SPI < 0.70$). However, their use of sectors was more evenly distributed when it was cold than when it was either mild or warm. The ring-tailed lemurs' SPI was 0.49 when it was cold (92% of time spent in 6 sectors), compared to 0.51 when it was mild (95% of time spent in 6 sectors) and 0.60 when it was warm (93% of time spent in 5 sectors). The

red ruffed lemurs' SPI was 0.49 when it was cold (94% of time spent in 7 sectors), compared to 0.60 when it was mild (92% of time spent in 5 sectors) and 0.66 when it was warm (90% of time spent in 4 sectors).

4.3. Use of levels

4.3.1. Enrichment effect on lemurs' use of levels

The lemurs' use of outdoor space subdivided by level and enrichment period is shown in Fig. 15. All through the study, the ring-tailed lemurs were present in level 0 around 60% of the time and predominately in level 1 for the rest of their time outdoors. They rarely used levels 2 or 3 during any period. The differences in the ring-tailed lemurs' use of levels among periods were never significant ($\chi^2_{(3)}$, $p > 0.05$). However, they used level 0 slightly less and level 1 slightly more during the enrichment periods than during the baseline.

The red ruffed lemurs used level 1 more than 70% of the time during all three periods, with the remaining 30% divided among the other three levels. They usually spent a larger amount of time in level 3 than levels 2 or 0. Like the ring-tailed lemurs, the differences in the red ruffed lemurs' use of levels among periods were never significant ($\chi^2_{(3)}$, $p > 0.05$). However, the differences between both enrichment periods were closer to being statistically significant ($\chi^2_{(3)} = 6.67$, $p = 0.083$). The red ruffed lemurs used level 1 the least and level 3 the most during the structural enrichment period. Moreover, they used level 0 notably more during the enrichment periods than during the baseline.

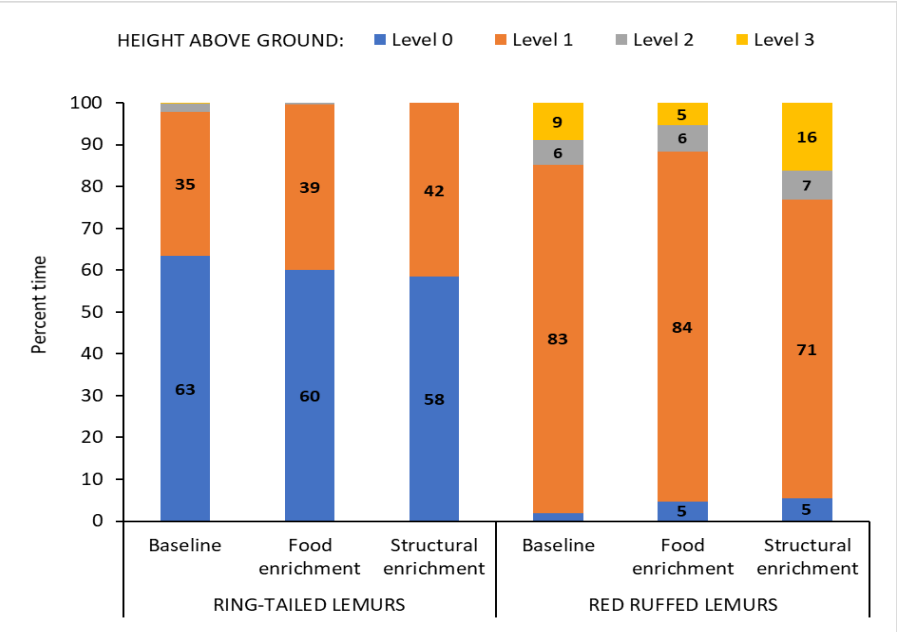

Fig. 15. Lemurs' use of outdoor space subdivided by level and enrichment period.

The lemurs' use of outdoor space by level was never evenly distributed ($0.60 < SPI < 0.80$). However, there were some species-specific differences. The way in which the ring-tailed lemurs' use of levels was distributed did not vary much among periods (SPI: 0.64-0.67). In contrast, the red ruffed lemurs' use of sectors was more evenly distributed during the structural enrichment period (SPI: 0.62) than during either the food enrichment period or the baseline (in both cases SPI: 0.78).

4.3.2. Visitor effect on lemurs' use of levels

The lemurs' use of outdoor space subdivided by level and visitor presence is shown in Fig. 16. The differences between the ring-tailed lemurs' use of levels with visitors and with no visitors were not significant ($\chi^2_{(3)} = 2.62$, $p > 0.05$). However, the ring-tailed lemurs used level 0 around 20% less and level 1 around 25% more with visitors than with no visitors. They rarely used level 2 and almost never used level 3.

The differences between the red ruffed lemurs' use of levels with visitors versus no visitors were significant ($\chi^2_{(3)} = 9.00$, $p = 0.029$). The red ruffed lemurs used level 1 significantly less and levels 0, 2 and 3 significantly more with no visitors than with visitors.

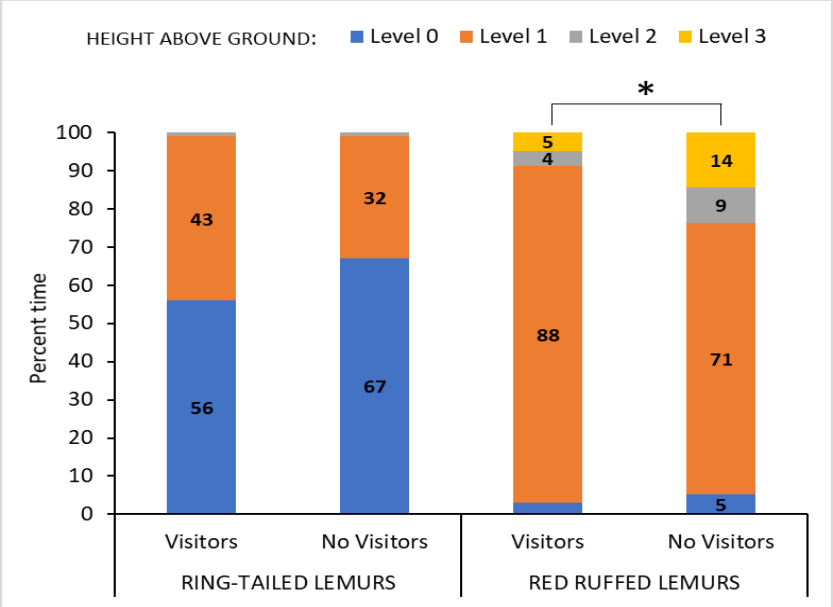

Fig. 16. Lemurs' use of outdoor space subdivided by level and visitor presence.
* $p < 0.05$ (χ^2 test)

The lemurs' use of outdoor space by level was never evenly distributed either with or without visitors ($0.60 < SPI < 0.85$). However, there were some species-specific differences. The way in which the ring-tailed lemurs' use of levels was distributed did not vary regardless of visitor

presence (always SPI: 0.65). In contrast, the red ruffed lemurs' use of sectors was more evenly distributed with no visitors (SPI: 0.62) than with visitors (SPI: 0.84).

4.3.3. Weather effect on lemurs' use of levels

The lemurs' use of outdoor space subdivided by level and weather is shown in Fig. 17. The differences in the ring-tailed lemurs' use of levels were significant between rainy and either cloudy ($\chi^2_{(3)} = 23.57$, $p < 0.01$) or sunny conditions ($\chi^2_{(3)} = 43.90$, $p < 0.01$). The ring-tailed lemurs used level 0 the most in sunny weather and the least in rainy conditions. The opposite was true for levels 1 and 2. They almost never used level 3, regardless of the weather conditions.

The differences in the red ruffed lemurs' use of levels were strongly significant between sunny and rainy conditions ($\chi^2_{(3)} = 10.10$, $p = 0.018$). These differences were especially significant for levels 1, 2 and 3 ($\chi^2_{(2)} = 10.01$, $p < 0.01$). The red ruffed lemurs used level 1 the most in sunny weather and the least in rainy conditions. The opposite was true for levels 2 and 3. Their use of level 0 did not vary among weather conditions.

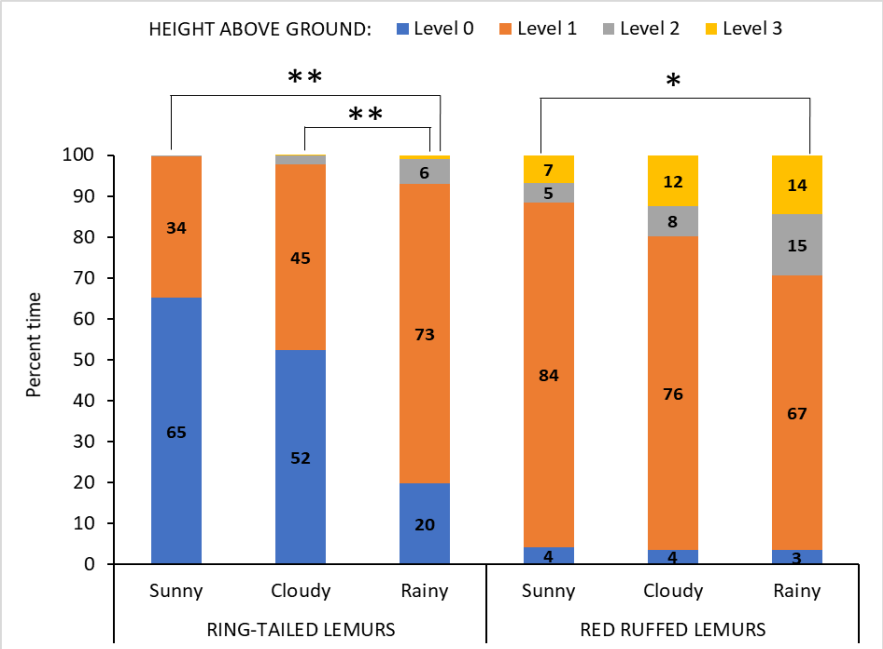

Fig. 17. Lemurs' use of outdoor space subdivided by level and weather.
* $p < 0.05$ / ** $p < 0.01$ (χ^2 test)

The lemurs' use of outdoor space by level was never evenly distributed among weather conditions ($0.55 < SPI < 0.80$). However, there were some species-specific differences. The way in which the ring-tailed lemurs' use of levels was distributed did not vary much among weather conditions (SPI: 0.64-0.66). In contrast, the red ruffed lemurs' use of sectors was

more evenly distributed in rainy (SPI: 0.56) than in cloudy (SPI: 0.69) or sunny conditions (SPI: 0.79).

4.3.4. Temperature effect on lemurs' use of levels

The lemurs' use of outdoors space subdivided by level and temperature is shown in Fig. 18. The differences in the ring-tailed lemurs' use of levels were significant between warm and either mild ($\chi^2_{(3)} = 9.34$, $p = 0.025$) or cold temperatures ($\chi^2_{(3)} = 19.23$, $p < 0.01$). The ring-tailed lemurs used level 0 the most when it was cold and the least when it was warm. The opposite was true for level 1. Throughout all periods, the ring-tailed lemurs rarely used level 2 and almost never used level 3.

The differences in the red ruffed lemurs' use of levels were significant between warm and cold temperatures ($\chi^2_{(3)} = 11.69$, $p < 0.01$). The red ruffed lemurs used level 1 the most when it was warm and the least when it was cold. The opposite was true for their use of levels 2 and 3. Their use of level 0 varied only slightly but they tended use it more in cold temperatures.

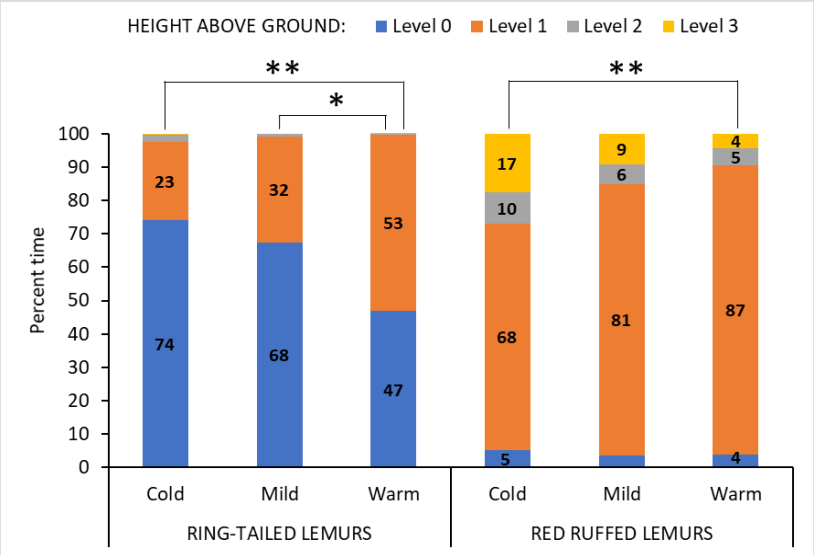

Fig. 18. Lemurs' use of outdoor space subdivided by level and temperature.
* $p < 0.05$ / ** $p < 0.01$ (χ^2 test)

The lemurs' use of outdoor space by level was never evenly distributed among temperature subcategories ($0.55 < SPI < 0.85$). However, there were some species-specific differences. The way in which the ring-tailed lemurs' use of levels was distributed did not vary much among temperature subcategories (SPI: 0.65-0.66). In contrast, the red ruffed lemurs' use of sectors was more evenly distributed when it was cold (SPI: 0.57) than either mild (SPI: 0.75) or warm (SPI: 0.82).

4.4. Behavior

4.4.1. Enrichment effect on lemurs' behavior

The distribution of the lemurs' behaviors subdivided by enrichment period is shown in Fig. 19. The ring-tailed lemurs' behavior was quite similar during all three periods, with around 50-60% of their time spent resting, around 20-25% of their time spent feeding/foraging, around 15-20% of their time in locomotion and 1-2% of their time interacting, which was mostly grooming and playing. The differences in the distribution of behaviors across periods were not significant for the ring-tailed lemurs ($\chi^2_{(3)}$, $p > 0.05$). However, there was slightly less resting and more locomotion during either enrichment period than during the baseline.

The differences in the distribution of the red ruffed lemurs' behaviors were significant between the structural enrichment period and either the food enrichment period ($\chi^2_{(3)} = 9.04$, $p = 0.029$) or the baseline ($\chi^2_{(3)} = 9.38$, $p = 0.025$). The red ruffed lemurs rested the most during the baseline and the least during the structural enrichment period. Their locomotion only changed during the structural enrichment period, when they moved significantly more than during either the food enrichment period or the baseline. They fed and foraged the most during the food enrichment period and the least during the structural enrichment period. Interaction did not vary notably across periods, although they interacted slightly more during the baseline than during either enrichment period.

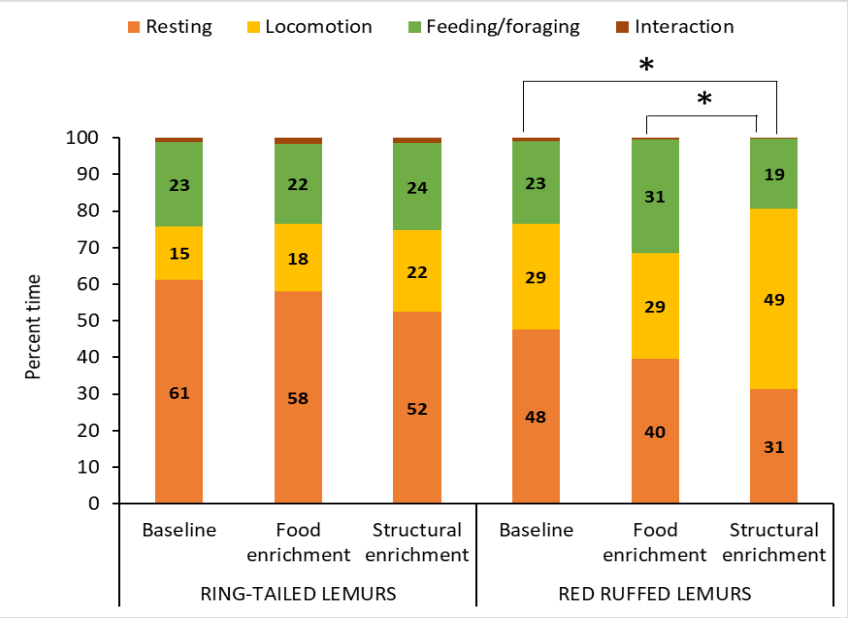

Fig. 19. Lemurs' behavior subdivided by enrichment period.
* $p < 0.05$ (χ^2 test)

4.4.2. Visitor effect on lemurs' behavior

The distribution of the lemurs' behaviors subdivided by visitor presence is shown in Fig. 20. The differences in the distribution of behaviors between visitors and no visitors were not significant for the ring-tailed lemurs ($\chi^2_{(3)} = 2.64$, $p > 0.05$). However, the ring-tailed lemurs rested less and moved and fed/foraged more with no visitors than with visitors. Their interaction was always very low, but they interacted slightly more when there were no visitors. The red ruffed lemurs' differences in distribution of behaviors between visitors and no visitors were significant ($\chi^2_{(3)} = 12.89$, $p < 0.01$). The red ruffed lemurs rested significantly less and moved significantly more with no visitors than with visitors. They also fed/foraged significantly less with no visitors than with visitors. They almost never interacted, regardless of visitor presence or absence.

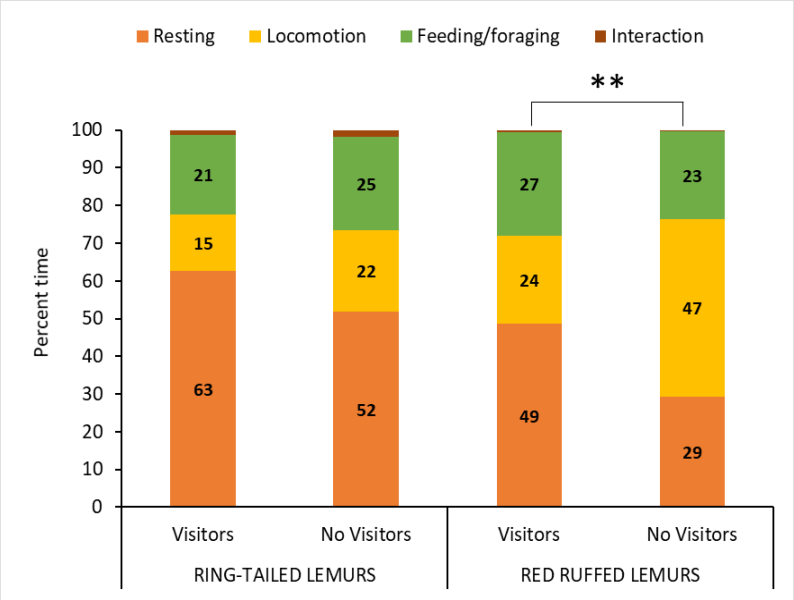

Fig. 20. Lemurs' behavior subdivided by visitor presence.
** $p < 0.01$ (χ^2 test)

4.4.3. Weather effect on lemurs' behavior

The distribution of the lemurs' behaviors subdivided by weather is shown in Fig. 21. The ring-tailed lemurs' differences in distribution of behaviors were only significant between sunny and rainy conditions ($\chi^2_{(3)} = 16.03$, $p < 0.01$). The ring-tailed lemurs rested the most in sunny weather and the least in rainy conditions. The opposite was true for locomotion and feeding/foraging. They rarely interacted with each other and never in rainy conditions.

Like the ring-tailed lemurs, the red ruffed lemurs' differences in distribution of behaviors were only significant between sunny and rainy conditions ($\chi^2_{(3)} = 8.48$, $p < 0.05$). The red ruffed lemurs rested the most in sunny weather and the least in rainy conditions. The

opposite was true for locomotion. They also fed/foraged the least in rainy conditions. They rarely interacted with each other, although slightly more in rainy than in either sunny or cloudy conditions.

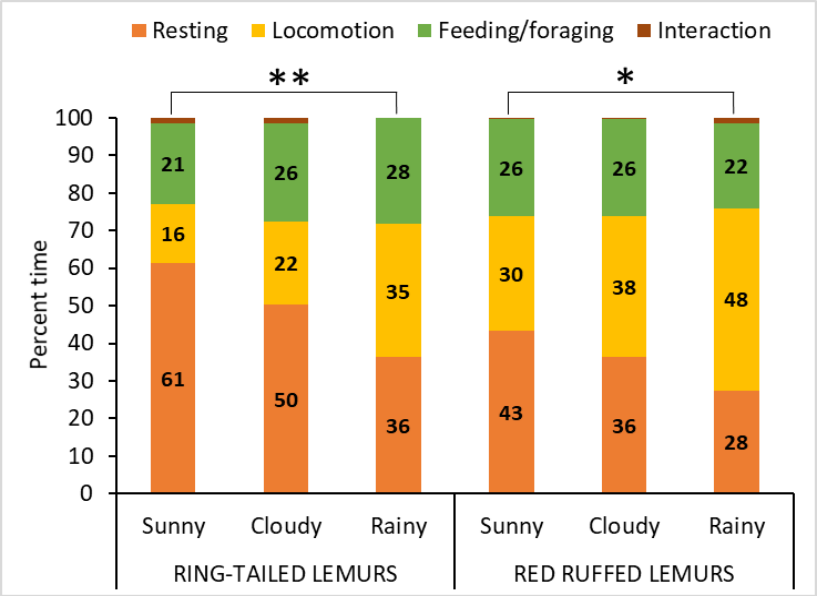

Fig. 21. Lemurs' behavior subdivided by weather.
* $p < 0.05$ / ** $p < 0.01$ (χ^2 test)

4.4.4. Temperature effect on lemurs' behavior

The distribution of the lemurs' behaviors subdivided by temperature is shown in Fig. 22. The differences in the distribution of behaviors among temperature subcategories were not significant for the ring-tailed lemurs ($\chi^2_{(3)}$, $p > 0.05$). However, the ring-tailed lemurs rested the most when it was warm and the least when it was cold. The opposite was true for locomotion. They also fed/foraged the least when it was warm. Interaction was always low and did not vary notably among temperature subcategories.

The red ruffed lemurs' differences in distribution of behaviors were significant between cold and either mild ($\chi^2_{(3)} = 10.46$, $p = 0.015$) or warm temperatures ($\chi^2_{(3)} = 21.51$, $p < 0.01$). The differences between cold and mild temperatures were also especially significant for resting and locomotion ($\chi^2_{(1)} = 10.41$, $p < 0.01$). The red ruffed lemurs rested the most when it was warm and the least when it was cold. The opposite was true for locomotion. Feeding/foraging did not vary notably among temperature subcategories. Interaction was always very low and it did not vary notably among temperature subcategories either.

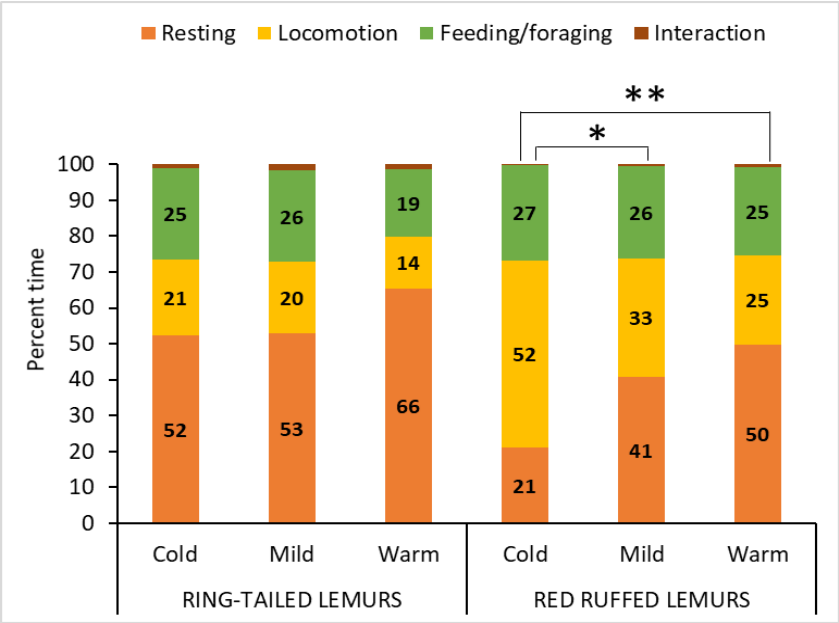

Fig. 22. Lemurs' behavior subdivided by temperature.
* $p < 0.05$ / ** $p < 0.01$ (χ^2 test)

5. Discussion

The results of this study demonstrate that enrichment, visitor presence, and meteorological conditions have a combined effect on the use of outdoor space and the behavior of ring-tailed lemurs and red ruffed lemurs housed in a mixed exhibit.

5.1. Outdoor presence

5.1.1. Ring-tailed lemurs' outdoor presence

The ring-tailed lemurs were outdoors the majority of the time during the baseline, which falls in line with their diurnal activity patterns (Bray et al., 2017). The unexpected decrease in their outdoor presence when enrichment was available may be explained by the combined effects of visitor presence and meteorological conditions. When visitors were present, the caretakers tended to lure the lemurs out with treats; considering that visitors were present the most during the baseline and second-most during the food enrichment period, this may partly explain why the ring-tailed lemurs were outdoors significantly more during those periods than during the structural enrichment period. In addition, ring-tailed lemurs seemed to prefer being outdoors when it was sunny and warm, and they avoided rain and cold. This may also explain why they were outdoors more often during the sunnier and warmer baseline and food enrichment periods than the rainier and colder structural enrichment period.

5.1.2. Red ruffed lemurs' outdoor presence

The red ruffed lemurs were outdoors less than the ring-tailed lemurs partially because data were collected during the daytime (9:00-17:00), whereas red ruffed lemurs are most active at dusk and dawn (Bray et al., 2017). The red ruffed lemurs' significant increase in outdoor presence during the food enrichment period confirms the powerful effect of food as an enrichment tool. As with the ring-tailed lemurs, the fact that they were outdoors less frequently during the structural enrichment period than the baseline or the food enrichment period may also be explained by the combined effect of visitor presence and meteorological conditions. Once again, when larger numbers of visitors were present, caretakers tended to lure out the lemurs with treats more often. While they seemed to be less sensitive to meteorological conditions than the ring-tailed lemurs, the red ruffed lemurs also tended to prefer going outdoors when it was sunny and warm This may also explain why they were outdoors more often during the sunnier and warmer baseline and food enrichment period than during the structural enrichment period.

5.2. Use of sectors

5.2.1. Ring-tailed lemurs' use of sectors

The ring-tailed lemurs' uneven use of sectors, which seemed to prioritize open areas and areas close to their house, may have indicated avoidance of central areas in the enclosure. The addition of enrichment in those unused sectors seemed to decrease their use of open areas and increase their use of the enriched sectors. The unexpected increase in use of areas close to their house may be partially explained by the fact that part of the enrichment was placed in a sector neighboring those areas. While the overall effect of visitor presence was not statistically significant, in the absence of visitors, the ring-tailed lemurs' use of sectors followed the same patterns of decreased use of open areas and increased use of enriched sectors observed when enrichment was added. This suggests that the presence of visitors may have deterred the ring-tailed lemurs from crossing the visitors' path to get to the food enrichment, but that it was not a significant nuisance to their overall use of sectors. On the other hand, meteorological conditions significantly affected the ring-tailed lemurs' use of sectors. They seemed to prefer sunnier and cooler conditions for use of open areas and when visiting the enriched sectors, and preferred cloudy conditions when approaching the red ruffed lemurs' house area, while avoiding open areas and staying close to their own house area when

it was rainy or too warm. The ring-tailed lemurs' unexpected presence in treed areas in rainy conditions may have been because rain caught them by surprise while they were feeding/foraging or chasing the red ruffed lemurs in those areas.

5.2.2. Red ruffed lemurs' use of sectors

Initially, the red ruffed lemurs' use of sectors was highly uneven, prioritizing the area close to their house and only sporadically venturing out to treed areas far away, while very rarely spending time in the central areas of the outdoor enclosure. This may have indicated extreme avoidance of most areas around the outdoor enclosure, which could have partially been due to a lack of boldness and/or slight apprehension about the ring-tailed lemurs' presence. However, the addition of enrichment significantly changed that pattern. Food enrichment encouraged them to leave their house area and venture out to the enriched sectors. Structural enrichment also made them bolder and they explored sectors further away from their house area more often, getting increasingly closer to the ring-tailed lemurs' house area. Visitor presence also seemed to have a significant effect on the red ruffed lemurs' use of sectors. When visitors were present, the red ruffed lemurs tended to remain in their house area more often and ventured out much less. Although the red ruffed lemurs kept visiting the enriched sectors, they did so less often when visitors were present. Meteorological conditions significantly affected the red ruffed lemurs' use of sectors. However, the effects were quite different than for the ring-tailed lemurs. The red ruffed lemurs preferred rainy and cold conditions for moving around the enclosure, while staying in their house area more often when it was sunnier and warmer. This pattern may indicate that they took advantage of the reduced presence of both visitors and ring-tailed lemurs in rainy and cold conditions to explore the outdoor enclosure more extensively.

5.3. Use of levels

5.3.1. Ring-tailed lemurs' use of levels

Throughout the study, the ring-tailed lemurs used the ground very often and rarely climbed above 10 m, while some studies in the wild have shown less use of the ground and extensive use of the upper canopy (Jolly, 1966; Budnitz and Dainis, 1975; Sussman, 1977). The ring-tailed lemurs' use of the ground in the present study may indicate habituation to a more terrestrial existence in a zoo setting. This pattern did not change significantly with the addition of enrichment, probably because food enrichment was placed in the same levels that

the ring-tailed lemurs already used the most during the baseline. The presence of visitors did not significantly affect the ring-tailed lemurs' use of levels. However, they spent more time on the ground when there were no visitors, which indicates a slight preference for using the ground when the enclosure is undisturbed. Meteorological conditions had a significant effect on the ring-tailed lemurs' use of levels. They preferred to be on the ground in sunny and cold conditions, mostly to rest and sunbathe, while climbing up to level 1 when it was rainy or too warm, mostly to seek shelter close to their house. When it was cloudy, they used the ground and the low canopy almost equally, mostly for moving around the enclosure. As with the use of sectors, their unexpected presence in higher levels of the canopy in rainy conditions may be because they were caught by surprise moving around the trees when it started to rain.

5.3.2. Red ruffed lemurs' use of levels

In previous studies, wild ruffed lemurs used the upper canopy most of the time and other levels of the forest less often (Britt, 1998; Vasey, 2004), while in the present study, they used the lower canopy the most. This contradictory result could be partially because areas with higher canopy were far away from the red ruffed lemurs' house, which forced them to cross the whole enclosure to reach those trees. Their initial skittishness could explain why they did not venture out to those areas very often. As with the ring-tailed lemurs, this pattern did not change significantly with the addition of enrichment, probably because food enrichment was also placed in the same level that they already used the most during the baseline. However, they seemed to get bolder during the enrichment periods, descending more often to the ground, maybe because they tried to get the food enrichment placed on that level. Moreover, the new structures available during the structural enrichment period helped the red ruffed lemurs reach sectors with higher canopy more easily, which may explain why their use of the highest canopy levels increased during that period. The presence of visitors seemed to significantly affect the red ruffed lemurs' use of levels. When no visitors were present, they tended to diversify their use of levels, but mainly rested in the low canopy close to their house when visitors were present. As with the ring-tailed lemurs, meteorological conditions had a strong effect on the red ruffed lemurs' use of levels, although the effect was less statistically significant. They preferred to climb up to the middle and high canopy in rainy and cold conditions, while mostly staying in the low canopy when it was sunny and warm, probably to avoid both visitors and the ring-tailed lemurs, or to be in the shade when it was too warm.

5.4. Behavior

5.4.1. Ring-tailed lemurs' behavior

The ring-tailed lemurs' resting (sunbathing or in a state of diurnal torpor), locomotion (exploring the enclosure or running back to their house) and feeding/foraging behaviors were similar to results obtained in previous studies carried out in the wild (Jolly, 1966; Sussman, 1977; Rasamimanana et al., 2006), in free-ranging conditions (Keith-Lucas et al., 1999) and in captivity (Goodenough et al., 2019). The very infrequent interaction displayed during the present study was also similar to the interaction measured in the wild by Rasamimanana et al. (2006), although Jolly (1966) and Sussman (1977) observed more interaction in the troops they studied. All these results may indicate that the lemurs in the present study have habituated well to their living conditions in the zoo. Their behavioral patterns did not change significantly when enrichment was added, although they tended to rest less and move more when enrichment was available, which may indicate that enrichment affects their behavior slightly, in line with the findings of previous studies (Maloney et al., 2006; Dishman et al., 2009; Shapiro et al., 2018). Other studies that included ring-tailed lemurs (Hosey and Druck, 1987; Chamove et al., 1988; Goodenough et al., 2019) or red ruffed lemurs (Mitchell et al., 1992) suggested that the mere presence of visitors increases locomotion in small arboreal primates. However, the overall results from the present study showed the opposite tendency. Collins et al. (2017) suggested that habituated lemurs may have a higher tolerance to visitors and that they only change their behavior significantly when large active groups are continuously present (which may be the case in the present study). Moreover, factors such as meteorological conditions may have combined with the effect of visitor presence, rendering visitor presence not statistically significant. This compound effect seems to be confirmed by the fact that the same pattern of increased resting and decreased locomotion behaviors occurred when it was sunny and warm, which coincidentally were also the predominant meteorological conditions when the zoo was open to visitors. The effect of meteorological conditions on the lemurs' behavior also aligns with previous studies on captive and free-ranging ring-tailed lemurs (Collins et al., 2017, Goodenough et al., 2019). Interestingly, the ring-tailed lemurs in the present study seemed to prefer cloudy and cooler conditions for feeding/foraging, maybe because meteorological conditions were neither pleasantly sunny or warm enough to sunbathe, nor inhospitable enough to seek shelter from rain or extreme heat. The unexpected increase in locomotion during rainy conditions could be explained by the ring-tailed lemurs run for cover when it started raining.

5.4.2. Red ruffed lemurs' behavior

The red ruffed lemurs' behavior differed notably from that of the ring-tailed lemurs. They may have exhibited more resting and less locomotion as a result of their initial skittishness when the ring-tailed lemurs were present, and that behavioral pattern may also explain why these results differed from previous studies that focused exclusively on ruffed lemurs, both in captivity and in the wild (Britt, 1998; Kerridge, 2005; Vasey, 2005). On the other hand, the fact that the red ruffed lemurs' feeding/foraging and interaction behaviors observed in the present study matched those studies' results, may also suggest habituation to this zoo setting. Some studies in ruffed lemurs suggest that feeding/foraging increases (Zimmerman and Feistner, 1996; Britt, 1998; Kerridge, 2005) and resting decreases (Kerridge, 2005) when food enrichment is available; the results from the present study match those findings. The fact that the red ruffed lemurs fed/foraged more when food enrichment was present and displayed more locomotion behaviors when structural enrichment was present – which helped them move more readily around the whole outdoor enclosure – strongly suggests that enrichment positively influenced their behavior. In contrast, visitor presence seemed to negatively influence their behavior, significantly increasing resting and decreasing locomotion. However, meteorological conditions may also partially account for those changes in behavior since the same pattern of increased resting and decreased locomotion was found when it was sunny and warm. Coincidentally, these were also the predominant conditions when the zoo was open to visitors. The red ruffed lemurs seemed to prefer rainy and cold conditions for moving around the enclosure, maybe because both visitors and the ring-tailed lemurs were less present in the outdoor enclosure under those meteorological conditions. Interestingly, the red ruffed lemurs interacted slightly more in rainy conditions, mostly because the male tried to mount the female more, which may have had a positive effect on their mating success.

5.5. Limitations

This study was carried out in a single zoo with a limited number of individuals. Further follow-up work should be conducted in multiple zoos with larger sample sizes to obtain deeper insight into the effect of enrichment, visitor presence, and meteorological conditions on captive lemurs' use of space and behavior. Moreover, it would be advantageous to compare the results of the present study with future studies in these same species when housed in separate enclosures to better understand the differences in lemurs' use of space and behavior between mixed-species and single-species exhibits.

Both species' atypical use of levels may have been reinforced by the fact that enrichment was placed in the levels the lemurs already used the most. Those were also the levels where sunbathing was most easily performed and food was most easily accessible. In addition, part of the enrichment was also placed in the same level as the entrances to their indoor enclosures, a place that was frequently used in less pleasant meteorological conditions. Due to logistical and legal constraints, it was not possible to place enrichment higher than 6-7 meters above ground level during this study. Future studies may benefit from placing food and structural enrichment in higher levels to better understand the effect of enrichment on the lemurs' use of levels.

Although care has been taken to avoid confounding factors, some variables were out of the researcher's control, such as husbandry regimes, feeding schedules and zookeepers' interactions. Moreover, considering that this study was only done at a group level as opposed to at an individual level, the composition of the lemur group may have influenced the overall results. More specifically, several intra-species differences were observed during the study. Although ring-tailed lemur females tended to feed first and lead the troop around, some male individuals challenged that pattern. Moreover, some males wandered about on their own and used the canopy areas more often. Older individuals tended to remain indoors or near their indoor enclosure more often. Younger individuals were more active, they explored, played and groomed more often. Playfulness, aggression and boldness also differed among individuals. As for the red ruffed lemurs, the female usually fed first, was bolder, and explored more, while the male was more agile and more communicative. All these inter-individual differences in both species may have played a role in their overall use of space and behavior in the mixed exhibit. Thus, using focal animal sampling and recording individual parameters such as age, sex or personality may help determine how important those aspects are in lemurs' use of space and behavior in captivity.

Due to seasonal variation in both visitor presence and meteorological conditions, future studies would also benefit from data collection during multiple seasons of the year to analyze long-term changes in behavior. Moreover, longer daily observation periods could provide insight into the effect of lemurs' internal circadian rhythms in their use of space and behavior in captivity.

5.6. Recommendations for future studies

All food enrichment devices were successfully used by both species of lemurs. However, the bottle spinner and the skewers were particularly effective in attracting the lemurs' attention. They were also the devices with which they interacted the longest, maybe because the lemurs needed to manipulate them longer to get the food reward. This suggests that the use of more manipulative devices may be a good way to increase the lemurs' use of enrichment and, thus, their outdoor presence in areas that are more visible to visitors.

The presence of food enrichment hanging on ropes encouraged the use of suspensory feeding postures. Surprisingly, those postures were not only used by the red ruffed lemurs, but also by the ring-tailed lemurs. Those postures had not been seen before in the ring-tailed lemurs when feeding on their own, which suggests that food enrichment may have motivated this behavior. Thus, hanging enrichment may be a good way to encourage a wider range of behaviors that could be beneficial to increase both the lemurs' welfare and the visitor experience.

Lemurs are social species that have complex interactions with other species in the wild. Socially complex mixed-species exhibits such as the one in the present study may be beneficial to their welfare because social interactions enhance the lemur's natural behaviors, provide them with cognitive challenges, and increase their activity levels (e.g., Leonardi et al., 2010; Veasey and Hammer, 2010). Mixed-species exhibits may also help maximize use of space and create a more engaging display for visitors. Before the study began, when the zoo was closed to visitors and no zookeepers were in the enclosure, only one species was allowed access to the outdoor enclosure at a time. Throughout the study, however, both species had simultaneous access to the outdoor enclosure. At first, the red ruffed lemurs appeared to avoid using the outdoor enclosure when the ring-tailed lemurs were around. After a few weeks of coexistence and especially after having been encouraged during the enrichment periods, the red ruffed lemurs explored the outdoor enclosure more and interacted more with the ring-tailed lemurs. Allowing both species to share the outdoor space for longer periods of time appeared to boost the red ruffed lemurs' confidence. They became bolder and less skittish. Meanwhile, the ring-tailed lemurs chased the red ruffed lemurs less, which suggested that they had become more accustomed to the red ruffed lemurs' presence and that cohabitation may have improved. Previous studies in primates have already concluded that careful enclosure design and the right environmental enrichment can promote beneficial interactions between species housed in a mixed exhibit (Pearson et al., 2010; Buchanan-Smith et al., 2013). Thus, future monitoring of changes in the lemurs' behavior while sharing the outdoor

space for longer periods of time may help confirm the beneficial or detrimental effects of encouraging this kind of mixed exhibit.

5.7. Conclusion

This study found inter-species differences in the use of space and behavior between ring-tailed lemurs and red ruffed lemurs. It also showed that enrichment, visitor presence and meteorological conditions had a complex combined effect on the lemurs. Enrichment proved to be a successful tool for increasing the lemurs' presence in underutilized sectors of the outdoor enclosure, thus making the lemurs more visible to the visitors. Moreover, meteorological conditions strongly affected the lemurs' use of space and behavior, while visitor presence had a weaker effect. Future enclosure designs should take all these parameters into account.

6. Societal and ethical considerations

This study complies with the American Society of Primatologists' "Principles for the Ethical Treatment of Non-Human Primates", Directive 2010/63/EU of the European Parliament and of the Council "on the protection of animals used for scientific purposes", and the Swedish "Animal Welfare Act" (2018:1192).

Throughout the study, the lemurs were always free to interact of their own accord with the enrichment provided. I was careful not to interfere in the lemurs' daily activities while I conducted all observations, and there was no indication that my presence caused any stress in any of the study individuals.

Studies on lemurs' use of space and behavior can help design more species-appropriate enclosures, thus improving the welfare of lemurs in captivity. Moreover, an enclosure that encourages a broader use of space and the expression of species-specific behaviors in captive lemurs can enhance the educational role of zoos and raise visitor awareness of the importance of wildlife conservation, especially for endangered species such as the ones in this study.

7. Acknowledgements

I would like to thank my supervisor, Matthias Laska, for his support and feedback. Many thanks to my co-supervisor, Ana Salomonsson, and the team at Furuviksparken for letting me collect data in the zoo facilities. Finally, I would like to include a special mention in thanks to Rebecca Reddin for her support and feedback throughout this project.

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Appendix

Table A.1. Lemur information.

Name	Relationship	Ranking	Sex	Age	Place of birth
Ring-tailed lemurs (RT)					
Bi	Mother of Ester, Holger, Lily & Vide	Matriarch	Female	18	Gute Zoo
Lily	Daughter of Bi & Leo (gone) Sister of Vide	2nd (next matriarch)	Female	2	Furuvik
Ester	Daughter of Bi Twin sister of Holger	3rd	Female	14	Furuvik
Vide	Son of Bi & Leo (gone) Brother of Lily	4th	Male	1	Furuvik
Holger	Son of Bi Twin brother of Ester	5th	Male	14	Furuvik
Albin	Son of Sofia & Voto (both gone) Twin brother of Alfred	6th	Male	12	Furuvik
Alfred	Son of Sofia & Voto (both gone) Twin brother of Albin	7th	Male	12	Furuvik
Germund	Son of Bell (gone)	Low	Male	14	Furuvik
Josef		Low	Male	16	Tropikariet
Red ruffed lemurs (RR)					
Mandry			Female	6	Twycross Zoo
Mangoro			Male	5	Wuppertal Zoo

Pictures of the study animals

Bi

Lilly

Vide

Ester

Holger

Josef

Albin

Alfred

Germund

Mandry

Mangoro

Pictures of the different sectors

Sector A

Sector B

Sector C

Sector D

Sector E

Sector F

Sector G

Sector H

Sector I

Sector J

Table A.2. Total amount of data points collected for each species in each period.

	Ring-tailed lemurs	***Red ruffed lemurs***
Baseline	9,971	1,166
Food enrichment	9,187	1,642
Structural enrichment	6,558	926
TOTAL	25,716	3,734