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# Effects of Enclosure and Environmental Enrichment on the Behaviour of Ring-Tailed Lemurs (*Lemur catta*)

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**Abstract:** Environmental enrichment is widely used to improve the quality of life of animals under human care. To successfully implement enrichment programs, it is important to evaluate their effect in different enclosure types since housing conditions may change depending on external factors, such as husbandry, management, or seasonal variation. This study investigates how ring-tailed lemur (*Lemur catta*) behaviour changes with the availability of enrichment items and the type of enclosure the animals are housed in. Through observations, we compared the behaviour of the lemurs in an indoor and outdoor enclosure, both without and with enrichment items. Although we observed enrichment effects, we found that enclosure type had a bigger effect on the lemurs' behaviour. Additionally, behavioural changes induced by enrichment items differed between indoor and outdoor enclosures. These results indicate that the effectiveness of enrichment items may depend on the enclosure in which they are provided and consequently suggest that the impact of these programs should not be generalised over enclosure types. This highlights that the evaluation of environmental enrichment programs remains important when optimising zoo animal welfare.

**Keywords:** enclosure type; enrichment; primate; welfare; zoo-housed

## 1. Introduction

Over the last decades, zoological institutions have made major efforts in promoting positive animal welfare. Good animal welfare can be considered as a balance between positive and negative experiences, dominated by positive experiences and where the animal can exert control over the negative experiences [1]. Environments that provide complexity, novelty, choice, and a sense of control provide animals with a variety of opportunities to experience different levels of (dis)comfort, interest, and confidence [1,2]. Aiming to provide these key factors ultimately contributes to the animal's welfare.

One way zoos aim to create stimulating and complex environments for the animals under their care is by providing environmental enrichment. There are numerous definitions for environmental enrichment, but all incorporate the idea that the environment of the animal is enhanced by providing variation in stimuli or creating opportunities of choice [3] while taking into account the species' behavioural biology and natural history [4]. Environmental enrichment is, therefore, a broad term and has many forms that can be categorised as feeding, tactile, structural, auditory, olfactory, visual, social, human-animal, and/or cognitive enrichment [5]. As a result, enrichment is one of the major topics within animal welfare science [6]. Goals of enrichment typically include, but are not limited to: (a) increase the diversity and performance of species-appropriate behaviours, (b) encourage space use in the enclosure, (c) reduce the presence of, and prevent the development of abnormal behaviours, and (d) increase the ability to cope with challenges [2,7].

Evaluation of enrichment programs is essential as many factors influence the effectiveness of enrichment items [4,8]. A recent development in the field of animal welfare is the 24/7 welfare approach that advocates for an inclusive perspective across day and night, weekdays and weekends, and seasons [9]. Yet, despite the significance of enrichment programs, current evaluations are often conducted within one enclosure type, even though zoo animals regularly rotate between public-facing enclosures and off-exhibits for management reasons, or between indoor and outdoor enclosures based on seasonal variations [9]. There is often substantial difference between such exhibits in terms of enclosure size, complexity, and degree of variation, which affects the behaviour of animals [10–12], social dynamics in group-living species [13], and possibly the degree to which individuals interact with enrichment items [14]. Following the 24/7 welfare approach, the evaluation of enrichment programs in different enclosure types is therefore necessary to improve its effectiveness and ultimately optimise zoo animal welfare [15].

Closely-related species show great variation in how they cope with captive settings [16] and institutions should also aim to tailor enrichment programs to the needs of the species (e.g., Hamilton et al. [17]). Within the order of primates, lemurs are among the most endangered species [18] and populations under human care could contribute to the species' survival in the future [19]. Previous lemur enrichment studies found that in response to food-based enrichment, general activity patterns and foraging behaviour increased to similar levels as their wild conspecifics [19–22]. Olfactory enrichment items may also be of interest for lemurs as they have highly developed scent glands and use olfactory cues extensively in the wild [23,24]. However, despite its apparent relevance for lemur species, olfactory stimulation is not as commonly applied in enrichment programs, and its effectiveness is not always as pronounced compared to food-based enrichment items [25,26].

In this study, we aim to better understand the effect of environmental enrichment by exploring how ring-tailed lemur (*Lemur catta*) behaviour in a zoo-setting is affected by (1) the availability of environmental enrichment and (2) the type of enclosure the animals are kept in. Based on enclosure size and complexity, we expect to find higher levels of inactivity and higher levels of self-directed and affiliative behaviours in the indoor enclosure compared to the outdoor enclosure [10]. We hypothesise that providing enrichment will stimulate active behaviours, such as locomotion and exploration, and lower levels of self-directed behaviours [19–22]. Yet, we predict to find a stronger enrichment effect in the, less stimulating, indoor enclosure than in the outdoor enclosure [14].

## 2. Materials and Methods

### *2.1. Ethical Statement*

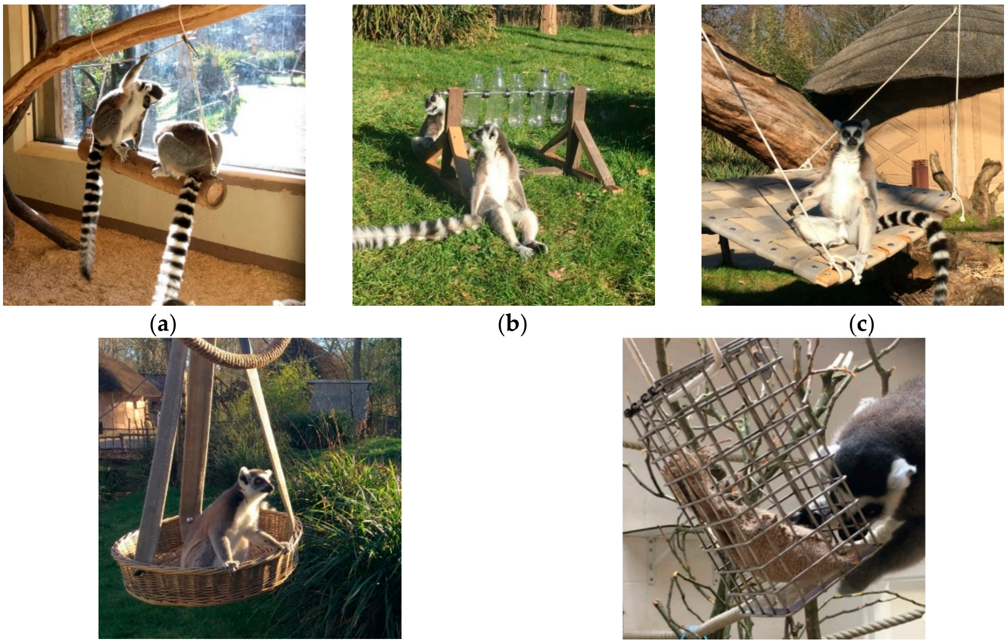
This study was conducted in compliance with all relevant Belgian and European legislation, and in agreement with international and scientific standards and guidelines. Due to the non-invasive character of the study, and absence of any potential discomfort, our study does not meet the definition of an animal experiment, as mentioned in Chapter I Article 16 of the Belgian Act on the protection and wellbeing of animals. Consequently, the Royal Zoological Society of Antwerp waived the requirement for formal approval of this study. Enrichment items used in this study were evaluated and approved by the veterinarian, curator, and keeper coordinator of ZOO Planckendael, who furthermore endorsed this study.

### *2.2. Subjects and Housing Conditions*

Behavioural data were collected between October 2018 and April 2019 on a group of six ring-tailed lemurs (four females, ages 1, 3, 8 and 14; and two males, ages 2 and 6) housed in ZOO Planckendael, Belgium. The ring-tailed lemurs were housed in an indoor enclosure of 48 $m^2$, consisting of five interconnected rooms furnished with climbing structures and the floors were covered with sawdust. The visitors could see the lemurs in one of the indoor enclosures through a large window while the other four enclosures were off-exhibit. When weather conditions permitted, the lemurs had access to an outdoor walk-through enclosure of 545 $m^2$, which included natural substrates such as grass, a pond, natural vegetation, and additional climbing structures. Visitors were able to enter the outdoor enclosure and walk along a visitor pathway. A keeper was always present to ensure that the animals were not touched nor fed. During opening hours, the lemurs were kept inside when temperatures dropped below 5 °C, while above 15 °C, they were kept outside. At any temperature in-between these thresholds, the lemurs got open access and were given the choice of either staying in or going out. During closing hours of the zoo, the lemurs were housed indoors when temperatures were too low, and otherwise had access to their outdoor enclosure. The ring-tailed lemurs shared the outdoor enclosure with one black lemur (*Eulemur macaco*) but were never housed together indoors.

### 2.3. Enrichment Items

We created five enrichment types that were novel to the lemurs (Figure 1). Enrichment items were selected to target a range of behaviours and included tube swings, bottle puzzles, hammocks, and baskets, which were food-based and contained a third of the daily lemur diet consisting of fresh vegetables, rice, and commercially available monkey chow. We also used olfactory enrichment items such as scented bags, which were made of jute pockets filled with, for example, coffee, fruit tea, animal hair (camel, sheep, and horse), herbs or spices (basil, pepper, and ginger). Of all item types, at least two items were made: one natural-looking version and one artificial-looking version, totalling 10 unique enrichment items. The distinction between artificial and natural-looking enrichment items was part of another study, but for this study, we do not distinguish between the two.



(**a**) (**b**) (**c**) (**d**) (**e**)

**Figure 1.** The enrichment items used in the study, including (**a**) tube swings, (**b**) bottle puzzles, (**c**) hammocks, (**d**) baskets and (**e**) scented bags.

### 2.4. Procedure

We considered two conditions during this study, a baseline condition, and an enrichment condition. During the baseline condition, no novel enrichment items were provided, apart from structural enrichment such as ropes and fresh branches with foliage, which always remained available. During the enrichment condition, we introduced the novel enrichment items to the lemurs in addition to their usual enrichment items. Each day, we provided the lemurs with two items of two different enrichment types, totalling four items at a time to avoid competition. These enrichment type combinations were counterbalanced between days to maintain a degree of novelty. Enrichment items were provided at the start of each observation session and remained available for the entire observation period.

### 2.5. Observations

We developed an ethogram based on preliminary observations and existing literature, which included 26 behavioural items that were grouped in ten behavioural categories (Table 1). We conducted 60-min observation sessions using instantaneous scan sampling every five minutes to score the behaviour of each individual lemur [27]. We did not consider the black lemur in this study as this individual transferred to another zoo before the end of the study period. Baseline behavioural data were collected indoors over 25 days and outdoors over 17 days. After this baseline period, we commenced the enrichment condition, in which we provided enrichment items over 25 days indoors, and 17 days outdoors. Behavioural data were collected between 10:00 and 17:00 for four days per week. Indoor observations were performed from the keepers' corridor and outdoor observations were done by moving through the enclosure to obtain the best view of the lemurs. The lemurs were habituated to the presence of the observers during the preliminary observations. All observations were recorded using ZooMonitor [28,29] by two observers who reached an interobserver reliability of >90%.

**Table 1.** Behavioural ethogram used during the study, with behavioural categories, its included behaviours and their description.

| Category | Behaviour | Description |
|---|---|---|
| Abnormal | Stereotypic walking | Walking the same route repeatedly. |
| Affiliation | Grooming | Licking or combing (using teeth) another's fur, sometimes using hands to part the fur. |
| | Mutual grooming | Two individuals simultaneously groom each other. |
| | Playing | Could include non-aggressive chasing, jumping, rolling around. |
| | Sexual behaviour | Mounting, mating, etc. |
| Agonistic | Chasing | Moving quickly towards and following another individual, causing it to flee. |
| | Fighting | Any succession of hitting, biting and/or grabbing, where two or more individuals each display at least one of the behaviours. |
| Enrichment | Manipulating enrichment item | Any form of behaviour targeted towards the enrichment items. This also includes structural enrichment items. |
| Exploration | Foraging | Actively looking for food using hands and mouth, by exploring surface or vegetation. |
| | Gnawing | Chewing on an item that is not food and is not eaten. |
| | Licking | Moving tongue up and down an item that is not their or another's body part. |
| | Sniffing | Placing the nose close to or on an object and smelling it. |
| Locomotion | Climbing | Moving up or down from a vertical surface, using its four limbs. |
| | Hanging | Hanging from an item in the environment, not touching a horizontal surface for support. |
| | Jumping | Moving from the ground or an elevated surface to the next, during which all four limbs are in the air at one point. |
| | Running | Moving quickly from one area to another by using four limbs. |
| | Standing on four legs | Using both feet and hands for support. Not any other body part is touching the ground/supporting surface (except for the tail). |
| | Standing upright | Standing on feet only, with the body upright. |
| | Walking | Moving from one area to another by using four limbs. |
| Resting | Resting | Sitting/laying down with eyes open or closed. |
| | Sitting | Placed on the base of the tail. |
| Species-specific | Scent marking | Marking an item of the environment with a scent gland. Lifting tail and rubbing genital area/scent glands against an object. |
| | Sunbathing | Sitting upright in an area with sunlight, with the belly-side directed towards the sun and arms open. |
| | Tail rubbing | Rubbing tail with the glands on forearms. |
| Self-directed | Self-scratching | Quickly moving fingernails or toenails up and down on one of its body parts. |
| | Self-grooming | Licking or combing (using teeth) own fur, sometimes using hands to part the fur. |
| Other | | Behaviours not listed above. |

*2.6. Analysis*

We summed the counts of each behaviour per subject per condition (i.e., indoor baseline, indoor with enrichment, outdoor baseline, and outdoor with enrichment). We created generalised linear mixed models (GLMMs) with a Poisson distribution that included subject identity as random effect to correct for repeated measures. We furthermore included random intercepts for day and for enrichment item combination. The total number of scans collected per individual and per condition was used as offset to control for unbalanced behavioural sampling across conditions. "Condition" (baseline vs. enrichment) and "enclosure" (inside vs. outside) were included as fixed factors to examine their effect on the activity budget of the lemurs. An interaction effect between condition and enclosure was included to examine potential differential effects of enrichment based on the enclosure type. Behaviours with very low frequencies (<1.00%; i.e., agonistic behaviours), and the category "other" were not analysed. Likelihood ratio tests and Chi-square distribution were used to compare the full model with the null model (Tables S1–S6, Supplementary Materials). All analyses were performed using R version 4.0.2 [30], with the GLMMs calculated using the lme4 package [31]. Diagnostic plots (residuals vs. fitted and QQ plots) were used to examine assumptions of normality and homogeneity of variances and we additionally tested uniformity and dispersion of the residuals using the DHARMa package [32].

## 3. Results

*3.1. Overall Activity Budget*

During the baseline condition, we completed 76 observation sessions indoors and 36 outdoors. For the enrichment condition, we completed 60 observation sessions indoors and 37 outdoors. On a global level, i.e., when considering all data of all individuals in all conditions, resting was most frequently observed (56.92%), followed by locomotion (14.79%), exploration (9.29%), self-directed (5.28%), enrichment (4.72%), species-specific (3.84%), affiliative (3.42%), other (1.72%), and agonistic (0.02%). Abnormal behaviour was not observed.

*3.2. Effect of Enrichment and Enclosure*

We examined potential effects of enclosure and/or enrichment on the occurrence of the behaviour of the lemurs (Figure 2a–d). The interaction between enclosure and enrichment significantly predicted the occurrence of resting ($\chi^2$ = 5.168, df = 1, $p$ = 0.023), exploration ($\chi^2$ = 32.678, df = 1, $p$ < 0.001) and species-specific behaviours ($\chi^2$ = 16.213, df = 1, $p$ < 0.001).

Using simple contrasts, we found that resting was lower outdoors than indoors, both without enrichment (z = −6.310, $p$ < 0.001) and with enrichment (z = −10.062, $p$ < 0.001) and lower in the outdoor enclosure with enrichment compared to when enrichment was absent (z = −2.429, $p$ = 0.015). There was no difference in resting indoor with or without enrichment (z = −0.328, $p$ = 0.743).

Exploration behaviour was more frequent outdoors than indoors, both when enrichment was provided (z = 11.616, $p$ < 0.001) and when enrichment was absent (z = 2.662, $p$ = 0.009). Exploration behaviour was lower indoors when enrichment was provided, compared to baseline levels (z = −5.736, $p$ < 0.001). Enrichment had no effect on exploration when given outdoors (z = 0.047, $p$ = 0.963).

Species-specific behaviours were higher outdoors compared to indoors during the enrichment condition (z = 6.460, $p$ < 0.001) and during the baseline condition (z = 6.061, $p$ < 0.001). Species-specific behaviours were also higher indoor when enrichment was provided, compared to the baseline condition (z = 4.339, $p$ < 0.001). No difference was found between the outdoor baseline and enrichment condition (z = 0.481, $p$ = 0.631).

We furthermore found main effects of enclosure (Figure 3a) for affiliation ($\chi^2$ = 57.545, df = 1, $p$ < 0.001), enrichment ($\chi^2$ = 15.221, df = 1, $p$ < 0.001), locomotion ($\chi^2$ = 121.799, df = 1, $p$ < 0.001), and self-directed behaviours ($\chi^2$ = 22.092, df = 1, $p$ < 0.001). Specifically, affiliation (z = 7.601, $p$ < 0.001) and self-directed behaviours (z = 4.685, $p$ < 0.001) were more often observed in the indoor enclosure than in the outdoor enclosure, while lower instances of enrichment (z = −3.597, $p < 0.001$) and locomotion (z = −10.595, $p < 0.001$) were observed indoors compared to the outdoor enclosure.

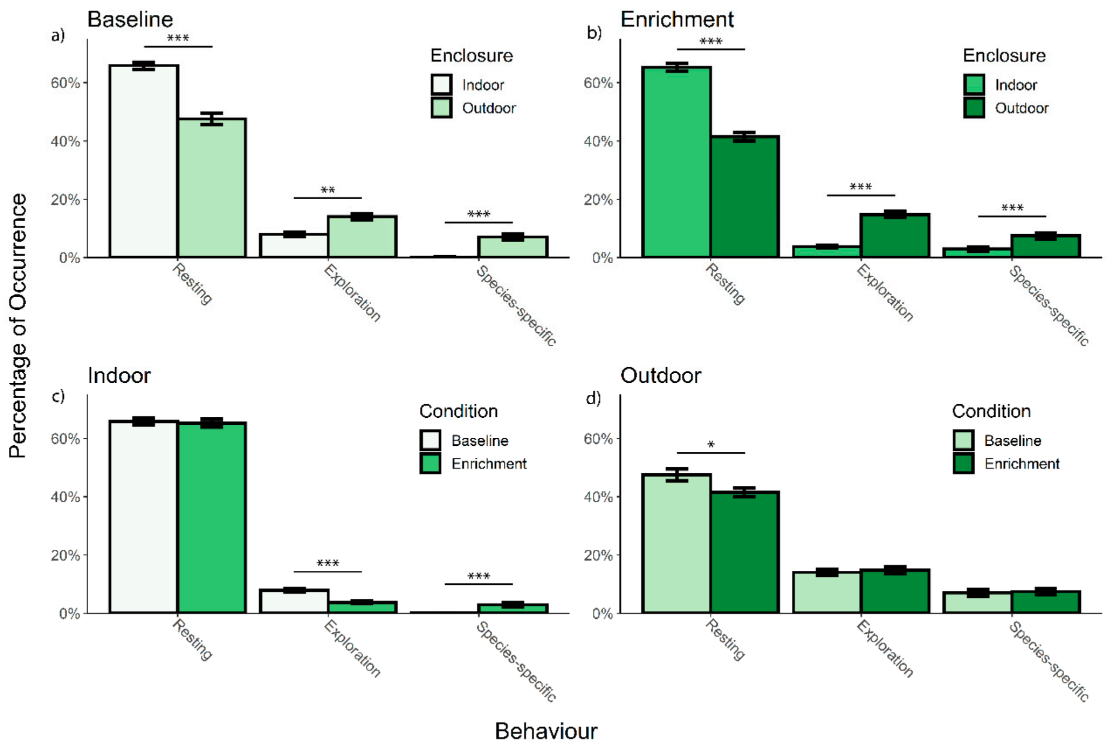



**Figure 2.** The percentage of occurrence (±SEM) for each behavioural category in the indoor and outdoor enclosure during the (**a**) baseline and during (**b**) enrichment condition; and during the baseline and enrichment condition in the (**c**) indoor enclosure and (**d**) outdoor enclosure. Comparisons were made using simple contrasts. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

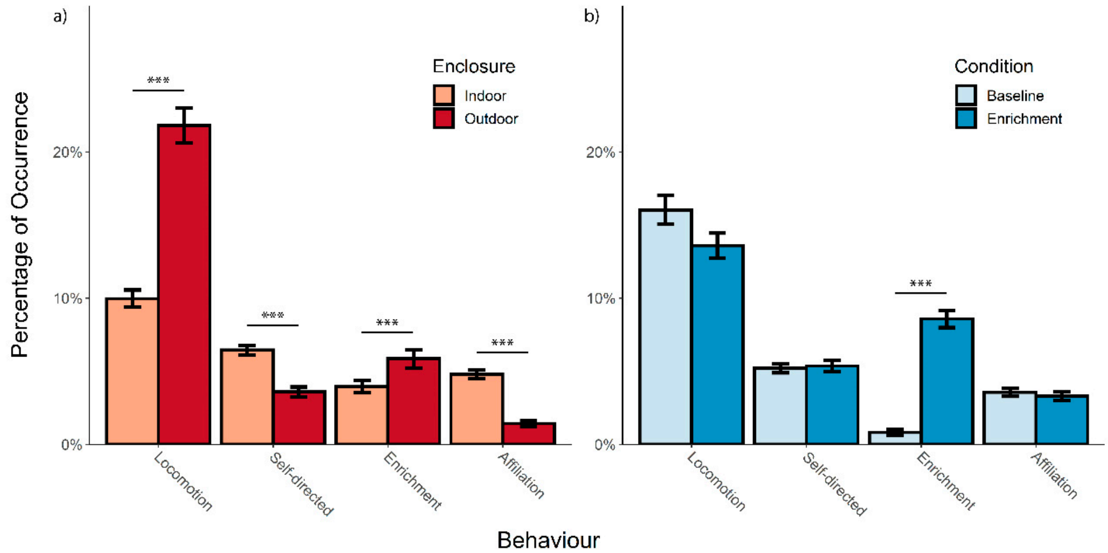



**Figure 3.** The percentage of occurrence (±SEM) for each behavioural category based on the (**a**) enclosure type and (**b**) enrichment provisioning. *** $p < 0.001$.

We also found a main effect of enrichment provisioning (Figure 3b) on enrichment ($\chi^2 = 98.555$, df = 1, $p < 0.001$) and a trend for locomotion ($\chi^2 = 3.416$, df = 1, $p = 0.065$). Obviously, enrichment provisioning was associated with higher frequencies of enrichment-related behaviours (z = 9.907, $p < 0.001$). Locomotion tended to be lower when enrichment was provided (z = −1.880, $p$ = 0.060). No main effect of enrichment was found for affiliation ($\chi^2$ = 0.622, df = 1, $p$ = 0.430) and self-directed behaviours ($\chi^2$ = 0.822, df = 1, $p$ = 0.495).

## 4. Discussion

This study aimed to examine the effect of enrichment and enclosure type on the behaviour of one group of zoo-housed ring-tailed lemurs. The behaviour of the lemurs was affected by both enrichment and enclosure type, although the effect of enrichment depended on the enclosure in which it was provided. Enclosure type appeared to have a bigger influence on the behaviour of the lemurs than enrichment provisioning. Next, we will discuss these results and extrapolate our findings in terms of animal welfare.

Across conditions, the ring-tailed lemurs were most often observed to rest and these levels were similar to those in another study with zoo-housed ring-tailed lemurs, which may suggest a species-typical level of resting behaviour in zoological institutions [21]. However, resting was less frequently observed in the outdoor enclosure. When enrichment was present outside, resting reached levels similar in wild and free-ranging populations [33,34]. Although natural behaviours are not unconditionally a sign of good welfare [35], excessive levels of inactivity in captive settings could potentially be an indicator of poor welfare [36] and may further result in health concerns, such as obesity. Enrichment only influenced resting levels when provided in the outdoor enclosure, but not in the indoor enclosure. The lemurs engaged more with the enrichment in the outdoor enclosure, something also observed in chimpanzees (*Pan troglodytes*) [14], which could have led to lower resting levels.

Locomotion was in general higher in the outdoor enclosure, but tended to decrease when enrichment was provided, regardless of enclosure type. This could reflect a trade-off between the time spent locomoting and interacting with the enrichment items [15]. Similarly, exploration also decreased when enrichment was given in the indoor enclosure. Outdoors, this effect was not present, and levels of exploration behaviour were generally higher than indoors. Outdoor enclosures typically have more environmental complexity, which is showcased in several aspects, including natural substrates, vegetation, interactions with other fauna, and weather conditions [9,37]. As such, outdoor enclosures provide sensory enrichment through additional external environmental factors that demand physical and cognitive responses and thus create opportunities for animals to exhibit a wide range of behaviours [15,38,39]. However, in less challenging environments, containing insufficient substrates, a trade-off between spontaneous exploration behaviour and interacting with enrichment items may occur.

We found that species-specific behaviours were more frequent in the outdoor enclosure. This can likely be attributed to increased sunbathing due to more access to direct sunlight [40], or more scent-marking as the outdoor enclosure was larger and therefore provided more substrates to which the lemurs could mark their scents. Interestingly, when housed indoors, species-specific behaviours increased when enrichment was provided, which was mostly due to increased sunbathing, which was possible through the window of the indoor enclosure. Alternatively, this may present an indirect enrichment effect, in which the presence of enrichment objects may alter the animal's behaviour, even if the animal did not directly interact with the object. At this stage, it is unclear if this effect is the result of the presence of enrichment items, or perhaps due to different weather conditions between the baseline and enrichment condition.

Apart from promoting species-appropriate behaviours, environmental enrichment is also often used to reduce behaviours that may indicate poor welfare, e.g., abnormal and self-directed behaviours [41–43], but see Neal and Caine [44]. We did not record abnormal behaviours throughout the study period, but we did observe self-directed behaviours albeit at relatively low levels. Self-directed behaviours did not reduce with the presence of enrichment, something that contrasts earlier studies that do report positive effects of enrichment to lower self-directed behaviours [45,46]. Rather than providing enrichment, having access to the outdoor enclosure did reduce the levels of self-directed behaviours in our study. This raises the question whether appropriate enrichment items were provided in this study. We presented different enrichment types at once to provide choice for the animals and to a range of behavioural categories. The lemurs spent approximately 9% of their activity budget interacting with enrichment items, suggesting that the lemurs showed sufficient interest in the enrichment items.

Lastly, we observed that affiliative behaviour such as grooming and social play were more frequent in the indoor enclosure than the outdoor enclosure. This could have been a tension-reduction strategy [47], where individuals engage more in affiliative behaviours in order to reduce tension, increase tolerance and decrease the chance of conflict [48]. The indoor enclosure was considerably smaller in size than the outdoor enclosure, and the observed heightened social behaviour could have been a coping strategy in response to reduced space availability. Additionally, food-based enrichment items are highly valued resources and could potentially elicit aggression when not well-distributed across the number of individuals in the group [49]. Although agonistic behaviour was too rarely observed to analyse, we did record some competition over enrichment items, despite always providing multiple items at a time. These cases were probably not recorded due to the nature of the sampling methods employed and are therefore not reflected in our data. We recommend future studies to tailor sampling methods to specifically investigate such research questions. Furthermore, we should highlight that we only observed one group and that the human-regulated social composition of this group could have influenced the observed differences in social behaviour. Our results, therefore, present a case study and since social composition, but also enclosure features and enrichment items, may greatly differ between zoos, generalising the result of this study over institutions should be avoided. To find species general patterns, it is recommended for future studies to sample multiple groups.

## 5. Conclusions

The effect of enrichment mostly depended on the enclosure in which it was provided. Enclosure type had a bigger impact on the behaviour of the lemurs, where activity levels increased in the outdoor enclosure while self-directed behaviours decreased. We did not identify which factors specifically contribute to these behavioural differences, but the increased size and environmental complexity of the outdoor enclosure likely contribute to these changes. Access to outdoor enclosures, and the accompanying environmental complexity, thus contributes to the welfare of ring-tailed lemurs. This highlights that when outdoor access cannot be guaranteed, it becomes crucial to provide sufficient environmental complexity and variation in indoor enclosures [50]. Depending on the geographic location of the institution, seasonal variation determines outdoor enclosure quality and quantity [9] and zoos should aim to optimise outdoor enclosure use for animals by providing shelter against weather conditions and by implementing temperature regulating features. Outdoor access is also determined by the presence of zoo staff unless open access between indoor and outdoor enclosures is available in the absence of staff. Open access, day and night, improves animal welfare [51] and is an integrated part of the 24/7 welfare approach that aims for a holistic framework to enhance animal welfare across the animal's life cycle and throughout day and night, weeks and seasons [9]. Hence, even when animals have access to outdoor enclosures, zoos should evaluate how to optimally make use of these enclosures.

**Supplementary Materials:** The following are available online at https://www.mdpi.com/article/10.3390/jzbg2020012/s1, Tables S1–S6: Full-null model comparisons.

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## References

1. Mellor, D.J. Updating Animal Welfare Thinking: Moving beyond the "Five Freedoms" towards "A Life Worth Living". *Animals* **2016**, *6*, 21. [CrossRef] [PubMed]
2. Buchanan-Smith, H.M. Environmental enrichment for primates in laboratories. *Adv. Sci. Res.* **2011**, *5*, 41–56. [CrossRef]
3. de Azevedo, C.S.; Cipreste, C.F.; Young, R.J. Environmental enrichment: A GAP analysis. *Appl. Anim. Behav. Sci.* **2007**, *102*, 329–343. [CrossRef]
4. Hoy, J.M.; Murray, P.J.; Tribe, A. Thirty years later: Enrichment practices for captive mammals. *Zoo Biol.* **2010**, *29*, 303–316. [CrossRef] [PubMed]
5. Maple, T.L.; Perdue, B.M. (Eds.) Environmental Enrichment. In *Zoo Animal Welfare*; Springer: Berlin/Heidelberg, Germany, 2013; pp. 95–117. ISBN 9783642359552.
6. Binding, S.; Farmer, H.; Krusin, L.; Cronin, K. Status of animal welfare research in zoos and aquariums: Where are we, where to next? *J. Zoo Aquar. Res.* **2020**, *8*, 1–9.
7. Mellen, J.; MacPhee, M.S. Philosophy of environmental enrichment: Past, present, and future. *Zoo Biol.* **2001**, *20*, 211–226. [CrossRef]
8. Alligood, C.; Leighty, K. Putting the "E" in SPIDER: Evolving Trends in the Evaluation of Environmental Enrichment Efficacy in Zoological Settings. *Anim. Behav. Cogn.* **2015**, *2*, 200–217. [CrossRef]
9. Brando, S.; Buchanan-Smith, H.M. The 24/7 approach to promoting optimal welfare for captive wild animals. *Behav. Processes* **2018**, *156*, 83–95. [CrossRef]
10. Ross, S.R.; Wagner, K.E.; Schapiro, S.J.; Hau, J. Ape behavior in two alternating environments: Comparing exhibit and short-term holding areas. *Am. J. Primatol.* **2010**, *72*, 951–959. [CrossRef]
11. Kurtycz, L.M.; Wagner, K.E.; Ross, S.R. The Choice to Access Outdoor Areas Affects the Behavior of Great Apes. *J. Appl. Anim. Welf. Sci.* **2014**, *17*, 185–197. [CrossRef]
12. Ross, S.R.; Calcutt, S.; Schapiro, S.J.; Hau, J. Space use selectivity by chimpanzees and gorillas in an indoor-outdoor enclosure. *Am. J. Primatol.* **2011**, *73*, 197–208. [CrossRef]
13. Koyama, N.F.; Aureli, F. Social network changes during space restriction in zoo chimpanzees. *Primates* **2019**, *60*, 203–211. [CrossRef] [PubMed]
14. Videan, E.N.; Fritz, J.; Schwandt, M.L.; Smith, H.F.; Howell, S. Controllability in Environmental Enrichment for Captive Chimpanzees (*Pan troglodytes*). *J. Appl. Anim. Welf. Sci.* **2005**, *8*, 117–130. [CrossRef] [PubMed]
15. Sha, J.C.M.; Ismail, R.; Marlena, D.; Lee, J.L. Environmental complexity and feeding enrichment can mitigate effects of space constraints in captive callitrichids. *Lab. Anim.* **2016**, *50*, 137–144. [CrossRef]
16. Clubb, R.; Mason, G. Captivity effects on wide-ranging carnivores. *Nature* **2003**, *425*, 473–474. [CrossRef] [PubMed]
17. Hamilton, J.; Fuller, G.; Allard, S. Evaluation of the impact of behavioral opportunities on four zoo-housed aardvarks (*Orycteropus afer*). *Animals* **2020**, *10*, 1433. [CrossRef] [PubMed]
18. Schwitzer, C.; Mittermeier, R.A.; Davies, N.; Johnson, S.; Ratsimbazafy, J.; Razafindramanana, J.; Louis, E.E., Jr.; Rajaobelina, S. *Lemurs of Madagascar: A Strategy for Their Conservation 2013–2016*; Bristol Conservation and Scienece Foundation: Bristol, UK, 2013.
19. Maloney, M.A.; Meiers, S.T.; White, J.; Romano, M.A. Effects of three Food Enrichment Items on the behavior of black lemurs (*Eulemur macaco macaco*) and ringtail lemurs (*Lemur catta*) at the Henson Robinson Zoo, Springfield, Illinois. *J. Appl. Anim. Welf. Sci.* **2006**, *9*, 111–127. [CrossRef]
20. Britt, A. Encouraging natural feeding behavior in captive-bred black and white ruffed Lemurs (Varecia variegata variegata). *Zoo Biol.* **1998**, *17*, 379–392. [CrossRef]
21. Dishman, D.L.; Thomson, D.M.; Karnovsky, N.J. Does simple feeding enrichment raise activity levels of captive ring-tailed lemurs (*Lemur catta*)? *Appl. Anim. Behav. Sci.* **2009**, *116*, 88–95. [CrossRef]
22. Fernandez, E.J.; Timberlake, W. Selecting and Testing Environmental Enrichment in Lemurs. *Front. Psychol.* **2019**, *10*, 1–12. [CrossRef]
23. Kappeler, P.M. Social status and scent-marking behaviour in *Lemur catta*. *Anim. Behav.* **1990**, *40*, 774–776. [CrossRef]

24. Kappeler, P.M. To whom it may concern: The transmission and function of chemical signals in *Lemur catta*. *Behav. Ecol. Sociobiol.* **1998**, *42*, 411–421. [CrossRef]
25. Baker, B.; Taylor, S.; Montrose, V.T. The effects of olfactory stimulation on the behavior of captive ring-tailed lemurs (*Lemur catta*). *Zoo Biol.* **2018**, *37*, 16–22. [CrossRef]
26. Vaglio, S.; Kaburu, S.S.K.; Young, C.; Pearce, R.; Smith, S.; Tompkins, B.; Elwell, E.; Fontani, S.; Marliani, G.; Accorsi, P.A. Effects of scent enrichment on behavioural and physiological indicators of stress in zoo primates—A preliminary study on red-ruffed lemurs and Lar gibbons. *bioRxiv* **2020**. [CrossRef]
27. Altmann, J. Observational Study of Behavior: Sampling Methods. *Behaviour* **1974**, *49*, 227–266. [CrossRef]
28. Wark, J.D.; Cronin, K.A.; Niemann, T.; Shender, M.A.; Horrigan, A.; Kao, A.; Ross, M.R. Monitoring the Behavior and Habitat Use of Animals to Enhance Welfare using the ZooMonitor App. *Anim. Behav. Cogn.* **2019**, *6*, 158–167. [CrossRef]
29. Ross, M.R.; Niemann, T.; Wark, J.D.; Heintz, M.R.; Horrigan, A.; Cronin, K.A.; Shender, M.A.; Gillespie, K. Zoo Monitor. Available online: https://zoomonitor.org (accessed on 16 October 2018).
30. R Core Team R: A Language and Environment for Statistical Computing. 2016. Available online: https://www.rstudio.com/ (accessed on 9 February 2021).
31. Bates, D.; Mächler, M.; Bolker, B.M.; Walker, S.C. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **2015**, *67*, 1–48. [CrossRef]
32. Hartig, F. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. Available online: https://cran.r-project.org/package=DHARMa (accessed on 9 February 2021).
33. Rasamimanana, H.; Andrianome, V.N.; Rambeloarivony, H.; Pasquet, P. Male and Female Ringtailed Lemurs' Energetic Strategy Does Not Explain Female Dominance. In *Ringtailed Lemur Biology: Lemur catta in Madagascar*; Jolly, A., Sussman, R.W., Koyama, N., Rasamimanana, H., Eds.; Springer: New York, NY, USA, 2006; pp. 271–295. ISBN 9780387341262.
34. Keith-lucas, T.; White, F.J.; Keith-lucas, L.; Vick, L.G. Changes in Behavior in Free-Ranging *Lemur catta* Following Release in a Natural Habitat. *Am. J. Primatol.* **1999**, *47*, 15–28. [CrossRef]
35. Browning, H. The Natural Behavior Debate: Two Conceptions of Animal Welfare. *J. Appl. Anim. Welf. Sci.* **2020**, *23*, 325–337. [CrossRef]
36. Fureix, C.; Kathleen, R. What can inactivity (in its various forms) reveal about affective states in non-human animals? A review. *Appl. Anim. Behav. Sci.* **2015**, *171*, 8–24. [CrossRef]
37. Honess, P.E.; Marin, C.M. Enrichment and aggression in primates. *Neurosci. Biobehav. Rev.* **2006**, *30*, 413–436. [CrossRef] [PubMed]
38. Swaisgood, R.R.; Ellis, S.; Forthman, D.L.; Shepherdson, D.J.; Atlanta, Z. Commentary: Improving Well-Being for Captive Giant Pandas: Theoretical and Practical Issues. *Zoo Biol.* **2003**, *22*, 347–354. [CrossRef]
39. Pines, M.K.; Kaplan, G.; Rogers, L.J. A note on indoor and outdoor housing preferences of common marmosets (*Callithrix jacchus*). *Appl. Anim. Behav. Sci.* **2007**, *108*, 348–353. [CrossRef]
40. Goodenough, A.E.; Mcdonald, K.; Moody, K.; Wheeler, C. Are "Visitor Effects" Overestimated? Behaviour in Captive Lemurs is Mainly Driven by Co-Variation with Time and Weather. *J. Zoo Aquar. Res.* **2019**, *7*, 59–66.
41. Maestripieri, D.; Schino, G.; Aureli, F.; Troisi, A. A modest proposal: Displacement activities as an indicator of emotions in primates. *Anim. Behav.* **1992**, *44*, 967–979. [CrossRef]
42. Bassett, L.; Buchanan-Smith, H.M. Effects of predictability on the welfare of captive animals. *Appl. Anim. Behav. Sci.* **2007**, *102*, 223–245. [CrossRef]
43. Mason, G. Stereotypies: A critical review. *Anim. Behav.* **1991**, *41*, 1015–1037. [CrossRef]
44. Neal, S.J.; Caine, N.G. Scratching under positive and negative arousal in common marmosets (*Callithrix jacchus*). *Am. J. Primatol.* **2016**, *78*, 216–226. [CrossRef]
45. Costa, R.; Sousa, C.; Llorente, M. Assessment of environmental enrichment for different primate species under low budget: A case study. *J. Appl. Anim. Welf. Sci.* **2018**, 1–15. [CrossRef]
46. Brent, L.; Belik, M. The response of group-housed baboons to three enrichment toys. *Lab. Anim.* **1997**, *31*, 81–85. [CrossRef]
47. De Waal, F.B.M. The Myth of a Simple Relation Between Space and Aggression in Captive Primates. *Zoo Biol.* **1989**, *1*, 141–148. [CrossRef]
48. Crast, J.; Bloomsmith, M.A.; Jonesteller, T. Effects of Changing Housing Conditions on Mangabey Behavior (*Cercocebus atys*): Spatial Density, Housing Quality, and Novelty Effects. *Am. J. Primatol.* **2015**, *77*, 1001–1014. [CrossRef] [PubMed]
49. Perdue, B.M.; Clay, A.W.; Gaalema, D.E.; Maple, T.L.; Stoinski, T.S. Technology at the Zoo: The Influence of a Touchscreen Computer on Orangutans and Zoo Visitors. *Zoo Biol.* **2012**, *31*, 27–39. [CrossRef] [PubMed]
50. Buchanan-Smith, H.M.; Badihi, I. The psychology of control: Effects of control over supplementary light on welfare of marmosets. *Appl. Anim. Behav. Sci.* **2012**, *137*, 166–174. [CrossRef]
51. Brown, J.L.; Carlstead, K.; Bray, J.D.; Dickey, D.; Farin, C.; Ange-van Heugten, K. Individual and environmental risk factors associated with fecal glucocorticoid metabolite concentrations in zoo-housed Asian and African elephants. *PLoS ONE* **2019**, *14*, e0217326. [CrossRef]