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Effects of Feeding Enrichment on the Behavior of Ex-Pet Ring-Tailed Lemurs (Lemur catta)

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Effects of Feeding Enrichment on the Behavior of Ex-Pet Ring-tailed Lemurs (*Lemur catta*)

by

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Dedication

I am dedicating this thesis to my grandma (mi abuela), who taught me compassion and hope.

Acknowledgements

I would like to sincerely thank both my advisors, Dr. Andrea Baden and Dr. Erin Ehmke, for their guidance and assistance leading to the completion of my thesis. I'm grateful for the support I received from the members of the Primate Molecular Ecology Lab at Hunter College. A special thanks to the Reniala Lemur Rescue Center for allowing me to conduct my research at the facility. Lastly, I would like to express my love and gratitude towards my family and friends for their constant support and encouragement.

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Abstract

Environmental enrichment is a prevailing tool used to enhance the welfare and well-being of captive species. Benefits of enrichment commonly range from promoting activity levels to reducing stereotypic/abnormal behavior. This study investigated the impact of two forms of feeding enrichment on the behavior of ring-tailed lemurs (*Lemur catta*) confiscated from the illegal pet trade. Three ring-tailed lemur pairs, each subject to three phases throughout the study, received a control treatment (metal bowl) during the first and last phases. However, each pair received one of three treatments throughout the middle phase: (1) a metal bowl, (2) a ground feeding enrichment device, and (3) a suspensory feeding enrichment device. I documented the behavior of each pair using an instantaneous scan sampling at one-minute time intervals to obtain the occurrence of selective behaviors. Results demonstrated that both forms of feeding enrichment had a significant impact on the behavior of captive ring-tailed lemurs. Moreover, implementing different forms of feeding enrichment generated different behavioral impacts, likely because ring-tailed lemurs distinctly spend nearly 30% of its time on the ground. This study emphasized the importance of providing captive species enrichment that require and encourage natural active behaviors. Further research in this field is needed to magnify enrichment benefits that improve and maintain the quality of care for species in captivity.

Keywords: ring-tailed lemurs, illegal pet trade, welfare, feeding enrichment

Introduction

Populating 90 countries throughout the Neotropics, Africa, and Asia, over half of the world's non-human primate species are threatened with extinction due to anthropogenic pressures (Estrada et al., 2018; Estrada et al., 2017). One of these countries, Madagascar, is the fourth-largest island (Irwin et al., 2010) and harbors more than 20% of the world's non-human primate species diversity (Schwitzer et al., 2014). Historically, this island's complex topography combined with its wind and ocean currents has generated an enormous amount of unpredictable climate variations. These variations, along with the years of isolation from continental landmasses, have led to extraordinary levels of uniqueness and endemism within the island's biota (Dewar & Richard, 2012; Irwin et al., 2010). Nevertheless, unsustainable activities continue to threaten the island's inhabitants at increasing rates, and are exacerbated by widespread poverty, political instability, and the ever-growing Malagasy population (Estrada et al., 2018; Irwin et al., 2010; Rakotomanana et al., 2013; Schwitzer et al., 2014). Therefore, Madagascar is one of the earth's most important biodiversity hotspots because of the significant presence of endemism and impending extinction risk (Estrada et al., 2018; Myers et al., 2000; Rakotomanana et al., 2013). Lemurs, the island's endemic primates, are the most imperiled mammalian group worldwide, with over 98% of lemur species at risk of extinction (IUCN, 2020).

Ring-tailed Lemurs

Ring-tailed lemurs (*Lemur catta*), recognized for their iconic black-and-white striped tails, are a flagship species for conservation and are among Madagascar's best-known lemur species. Moreover, ring-tailed lemurs are prevalent globally throughout zoos, research, and popular culture (LaFleur et al., 2017; Sauther et al., 2015). This lemur species is distinguished for its ability to survive and reproduce in a variety of habitats due to its behavioral and ecological flexibility.

Accordingly, ring-tailed lemurs can rebound from environmental extremes to natural disasters such as severe droughts. Populations of this lemur species were once widely spread across the southern regions of Madagascar (Goodman et al., 2006; Gould, 2006; Gould et al., 2003; Sauther et al., 2015). However, the first large-scale population estimates of ring-tailed lemurs revealed that nearly 20% of the population decreased from 1985 to 2000 (Sussman et al., 2006).

Subsequently, more evidence of local ring-tailed lemur extinctions and population declines have been emerging over the years because of the continuation of research on the census of several Malagasy sites. Habitat loss and forest fragmentation proceed to rise across ring-tailed lemur's geographical range on account of deforestation from charcoal production, slash-and-burn agriculture, and livestock grazing. Therefore, this lemur species is distributed unevenly across isolated forest fragments with low population densities. Although ring-tailed lemurs are capable of adapting and flourishing in harsh environmental conditions, they are not able to survive in absolutely degraded habitats for an extended period of time (Gould & Sauther, 2016; LaFleur et al., 2016). Furthermore, ring-tailed lemur populations encounter other sorts of anthropogenic threats, specifically the illegal pet trade (Gould & Sauther, 2016; LaFleur et al., 2019; Reuter et al., 2016; Reuter et al., 2019; Reuter & Schaefer, 2017a).

Illegal Pet Trade

Non-human primates often are prized as pets worldwide, where they are either bred in captivity or captured in the wild. When caught in the wild, non-human primates can be traded within national borders as well as exported to other countries. These captures, trades, and ownerships might be legal or illegal depending on where a non-human primate resides along with its status (Norconk et al., 2020; Reuter et al., 2019; Soulsbury et al., 2009). Notably, it has been illegal to capture, trade, and own lemurs domestically and internationally since 1962. The punishments one would receive for these illegal activities entail confiscation of pet lemur, a fine, and imprisonment (Ordonnance nº 60-128, 1962). Unfortunately, these illegal activities are still an ongoing problem within Madagascar even with the various punishments one could receive (LaFleur et al., 2019; Reuter et al., 2016; Reuter et al., 2019; Reuter & Schaefer, 2017a).

The lack of environmental law enforcement throughout the island contributes to the continuation of this threat (LaFleur et al., 2019; Reuter et al., 2016; Reuter et al., 2019). Additionally, the motivating factors in owning a lemur include symbols of status/wealth, companionship, and income (LaFleur et al., 2019; Reuter et al., 2018; Reuter et al., 2019; Reuter & Schaefer, 2017c). Regardless of the motivation of owning a lemur, lemur populations are impacted significantly since pet lemurs are sourced solely from the wild (LaFleur et al., 2015; LaFleur et al., 2019; Reuter et al., 2019). Thus, these lemurs are no longer aiding their native forests via seed dispersal or contributing to their wild population via reproduction. These are two significant consequences considering both play vital parts in the survival of species threatened with extinction (LaFleur et al., 2019).

Illegal lemur ownership is geographically spread across Madagascar; however, it appears to disproportionately affect certain lemur species (LaFleur et al., 2019; Reuter et al., 2016; Reuter et al., 2019; Reuter & Schaefer, 2017a; Reuter & Schaefer, 2017b). Ring-tailed lemurs are one of the most common lemur species to be owned as an illegal pet (LaFleur et al., 2019; Reuter et al., 2019; Reuter & Schaefer, 2017a; Reuter & Schaefer, 2017b). Infants and juveniles are usually targeted for extraction from the wild. The levels of these extractions in ring-tailed lemur populations of 500 or less adds additional pressure to a lemur species already dealing with other significant threats (LaFleur et al., 2019). As a result, this charismatic species of lemur is listed as Endangered under the IUCN Red List (Andriaholinirina et al., 2014). Despite the growing literature on the illegal pet trade, it is still not acknowledged as equally alarming as other anthropogenic threats. For this reason, there is a lack of urgency on the negative impacts of the illegal pet trade, particularly on the psychological and physiological problems lemurs develop due to poor captive conditions (LaFleur et al., 2015; LaFleur et al., 2019; Reuter et al., 2016; Reuter & Schaefer, 2016; Reuter & Schaefer, 2017b).

Welfare of Pet Lemurs

The care of legally captive species in various parts of the world generally involves providing appropriate nutrition, a sufficient amount of space, environmental enrichment, and similar social settings as to their wild counterparts (Mellor et al., 2015). Conversely, most of the captive conditions that illegal pet lemurs endure within Madagascar barely meet these basic care requirements (Reuter & Schaefer, 2016). Pet lemurs are often either kept in small-scale cages with limited freedom of movement or restrained to ropes, leashes, or chains (Reuter & Schaefer, 2016; Reuter & Schaefer, 2017b). These kinds of restraints could cause unintentional injuries (e.g., asphyxiation by strangulation), especially when they are too tight, long, or become tangled (Reuter & Schaefer, 2016). Pet lemurs are rarely socially housed, which is not ideal as most wild lemur species usually exist in social groups (Pride, 2005; Reuter & Schaefer, 2016). The diet of pet lemurs is commonly inconsistent with their wild counterparts' diets, such as various human food. The quantity of food given to pet lemurs depends on why they are owned; therefore, they could be both underfed and overfed. Pet lemurs owned as tourist attractions might run the chance of being overfed if tourists routinely feed them during interactions (Reuter & Schaefer, 2016).

Moreover, the risk of disease transmission, especially between lemurs and humans, may increase in spaces where they come in close contact with each other (Reuter & Schaefer, 2016). Aggression and stereotypic/abnormal behaviors (e.g., pacing due to restrictive cages) are regularly exhibited by pet lemurs (LaFleur et al., 2015; LaFleur et al., 2019; Reuter & Schaefer, 2016; Reuter & Schaefer, 2017b). Some might have certain body parts amputated or bones deliberately broken because of their aggression (LaFleur et al., 2019). Ultimately, illegal lemur ownership appears to often be short-lived for a range of reasons due to the owner's lack of understanding of how to care for a lemur (Reuter & Schaefer, 2016). There are, however, a few legal captive facilities in Madagascar that provide adequate care for confiscated illegally owned lemurs (LaFleur et al., 2015; LaFleur et al., 2019; Reuter & Schaefer, 2017b). Reniala Lemur Rescue Center (LRC) is a privately owned captive rehabilitation facility situated inside the Reniala Botanical Reserve in the Mangily region of Ifaty. The LRC rehabilitates confiscated illegally owned lemurs with the end goal of potentially releasing them back into the wild. Environmental enrichment is a husbandry practice that LRC provides for their lemurs to enhance the skills necessary for survival in the wild (LaFleur et al., 2015).

Feeding Enrichment

Environmental enrichment is a prevailing tool used to enhance the welfare and well-being of captive species. The benefits of implementing enrichment include: (1) promoting activity levels, (2) encouraging species-specific behaviors, (3) reducing stereotypic/abnormal behaviors, and (4) improving physical health. Additionally, successful enrichment allow captive species to exercise control over their environment (Maple & Perdue, 2013; Mellor et al., 2015; Young, 2003). These benefits are significant for maintaining a healthy and thriving captive population, especially for endangered species, as they could potentially contribute to their survival in the future (Shapiro et al., 2018). There are different forms of environmental enrichment, such as sensory, physical, social, nutritional, and cognitive enrichment (Maple & Perdue, 2013; Young, 2003). Several studies have examined the behavioral effects of enrichment on different captive non-human primates (e.g., Gronqvist et al., 2013; Robbins & Margulis, 2014). However, only a small number of those studies focused on lemurs and primarily investigated the effects of feeding enrichment (e.g., Dishman et al., 2009; Fernandez & Timberlake, 2019; Maloney et al., 2006; Shapiro et al., 2018; Sommerfeld et al., 2006).

One of the simplest forms of feeding enrichment, shown to be effective in increasing the activity levels of ring-tailed lemurs, involves reducing the visibility and accessibility of their diets. Another form of feeding enrichment deals with increasing the spatial complexity of diet presentations. Spatially separating diet presentations is shown to be effective in reducing undesirable behavior of ring-tailed lemurs. For instance, this form of arrangement likely decreases the chances of conflict occurring between individuals over access to their diets (Dishman et al., 2009). Although these simple feeding enrichments resulted in positive behavioral responses from ring-tailed lemurs, other forms of feeding enrichment might not elicit similar responses (Shapiro et al., 2018). One of the findings from a study, conducted by Shapiro et al. (2018), demonstrated that a feeding enrichment placed on the ground is more beneficial for captive ring-tailed lemurs (e.g., increasing locomotion & decreasing resting) than a suspensory feeding enrichment. Since this lemur species distinctly spends nearly 30% of its time on the ground (Gould, 2006), this possibly attributed to the effectiveness of the ground feeding enrichment. Therefore, it might be best to consider the distinct evolutionary and natural histories of a captive species for the purpose of providing an effective enrichment (Shapiro et al., 2018).

Specific Aims

The present study investigated: (1) the behavioral impact of feeding enrichment on captive ex-pet ring-tailed lemurs and (2) whether the behavioral impact varied based on the form of the feeding enrichment. Subject to three phases, three ring-tailed lemur pairs received a control treatment (metal bowl) during the first and last phases of the study. However, each pair received one of three treatments throughout the middle phase: (1) a metal bowl, (2) a ground feeding enrichment device, and (3) a suspensory feeding enrichment device. Both forms of feeding enrichment devices were hypothesized to significantly impact ring-tailed lemur behavior. I predicted that both devices would encourage device interaction and natural active behaviors (i.e., exploration, foraging, locomotion, & positive interaction) while reducing undesirable behaviors (i.e., resting & stereotypic behavior). Additionally, I hypothesized that the ground feeding enrichment device would have a greater behavioral impact than the suspensory feeding enrichment device. The semi-terrestrial behavior of this lemur species, along with the findings of previous studies (e.g., Shapiro et al., 2018), influenced this hypothesis. Specifically, I predicted that the ground feeding enrichment device would encourage more device interaction and natural active behaviors while reducing more undesirable behaviors.

Methods

Study Site and Subjects

Study subjects involved three pairs of captive ex-pet ring-tailed lemurs (*Lemur catta*). Table I summarizes information about each pair, including names, sex, and ages. Subjects were housed in pairs within an outdoor enclosure, which was a $64m^3$ structure subdivided into eight 2m x 2m x 2m units, at the Reniala Lemur Rescue Center (LRC). A metal frame supported the wire mesh roof and perimeter walls of the enclosure. Concrete/wire mesh wall dividers separated the units from each other. However, the dividers were outfitted with wooden/wire mesh hatches that provided the ability to either make units continuous or section them off. A concrete border surrounded the floor composed of the sandy substrate from the natural habitat of every unit. Each pair received access to two units along with a water bowl, wooden nesting boxes, wooden perches, and wooden platforms. There were a few reeds placed on top of the units to provide shade.

Table I. Collection of information on each pair

Pair	Name	Sex	Age
A*	Aciane	Male	Juvenile
	Lebandi	Male	Juvenile
B	Amjani	Male	Adult
	Gabri	Female	Adult
C	Billy	Female	Adult
	Maxi	Male	Adult

*Pair A had an additional ring-tailed lemur temporarily housed with them during the first week of the study

Only LRC caretakers were allowed to enter the enclosure for husbandry purposes. Caretakers accessed the enclosure via wire mesh entrance doors constructed at the front of every unit. Husbandry work consisted of feeding, changing water bowls, raking the sand floors, and cleaning outside the enclosure. Pairs were fed morning and afternoon diets, with distribution times varying daily. Each pair received approximately 0.5kg of mixed fruits and vegetables per feeding, which was usually scattered throughout their units. Occasionally the caretakers would collect branches from a variety of trees commonly eaten by the semi-wild ring-tailed lemur troop within the reserve and place them inside the pairs' units. The branches served as a form of environmental enrichment to encourage the ring-tailed lemurs to become accustomed to the natural resources they might encounter if released back into the wild. Additionally, the pairs were familiar with other forms of enrichment, such as hiding food in baobab fruit shells.

Treatments

Three treatments were administered in this study: (1) a metal bowl, (2) a ground feeding enrichment device, and (3) a suspensory feeding enrichment device (Figure I). The metal bowl was the control treatment, and therefore provided the baseline needed to compare the behavioral impact of the ground and suspensory treatments.

Figure I. The three treatments administered in this study: (a) Metal bowl, (b) Ground feeding enrichment device, and (c) Suspensory feeding enrichment device.

The ground treatment was a feeding enrichment device that consisted of a seesaw built out of wooden planks and a plastic storage container. Four 1" x 6" x 18" wooden planks created the base of the seesaw. The vertical beams of the base each had a hole drilled through them to fit a 3/8" floor flange. The floor flanges were secured into the beams by 1" nails. The purpose of the floor flanges was to attach both the vertical beams with a 3/8" x 8" pipe nipple. Moreover, the horizontal beams of the base were attached to the vertical beams by 2" nails. These beams provided stability and balance for the seesaw. The pivoting beam, a 1" x 6" x 36" wooden plank, had an attached plank beneath it. The attached plank's purpose was to prevent the pivoting beam from being overly steep for the subjects to sit, stand, and climb on. Before securing the two planks with 2” nails, a curve was carved on the side of the attached plank to allow the pipe nipple to pass through. Two ½” tube straps were secured beneath the pivoting beam by 1” nails and aligned with the carved curve. A plastic storage container was attached to the surface of the pivoting beam by 2” nails. The storage container had a removable lid that allowed food to be placed inside the container and sealed. Three holes were cut and sanded in a diagonal line on the lid, which were wide enough for the subjects to retrieve the food using their hands/mouths.

The suspensory treatment was a feeding enrichment device that consisted of a plastic basket, a hay net, and two paracords. A plastic basket was secured to the inside of a 42” hay net with jute twine. Food was placed inside the basket, and the top of the hay net was tied into a knot. The hay net offered several 2½” x 2½” holes, which were wide enough for the subjects to retrieve the food using their hands/mouths. Two knotted 72” paracords were each attached to opposite sides of the hay net and basket to offer the subjects another option of retrieving the food. The feeding enrichment was hung from the top of the units using a spring snap.

Ethogram

Before conducting this study, I developed and refined an ethogram that classified a spectrum of behaviors exhibited by ring-tailed lemurs. The ethogram incorporated behaviors described by Shapiro et al. (2018), Baker et al. (2018), and Maloney et al. (2006), as well as those observed at the Duke Lemur Center in Durham, North Carolina (USA). Table II alphabetically lists and defines the behaviors collected throughout this study.

Experimental Design

The study, conducted from July 8th to August 31st, 2019, consisted of three phases. During each phase, pairs were exposed to treatments for two hours in the morning every Monday through

Saturday. The availability of fruits and vegetables plus diet preparation by the caretakers affected the starting time for every morning session, which varied between 8:30 to 10:30 AM. One metal bowl/feeding enrichment device was provided for each subject.

Phase I: Pre-observational Phase

Phase I involved the pairs receiving the control treatment over a two-week period. Each pair was offered access to the morning diet in metal bowls for two hours. Bowls were filled with the morning diet before being placed inside a pair's units. The bowls of each pair were intentionally separated from one another (usually a bowl in each unit) when placed inside a pair's units.

Phase II: Experimental Phase

Phase II, which lasted four weeks, entailed each pair receiving one of the three treatments. Pair A received the control treatment and therefore continued to be offered access to the morning diet in metal bowls. Pair B received the ground treatment, while pair C received the suspensory treatment. Bowls/feeding enrichment devices were filled with the morning diet before being separately placed inside a pair's units.

Phase III: Post-observational Phase

Phase III occurred during the last two weeks of the study. Similar to Phase I, the pairs received only the control treatment. Bowls were filled with the morning diet before being separately placed inside a pair's units.

Behavioral Data Collection

Behavioral observations were video recorded during every morning session via Canon camcorders throughout all three phases. A camcorder was positioned on a tripod in front of each two units before morning diet preparations. Despite every effort made to ensure an unobstructed view of each pair, a small tree slightly blocked the view of a unit of the ground pair. Likewise, a concrete wall divider moderately blocked the view of a unit of the suspensory pair. Recording began before bowls/feeding enrichment devices were filled with the morning diet and placed inside a pair's units. The amount of time it took to set up these treatments inside a pair's units ranged from 30 seconds to four minutes. The camcorders were then allowed to run for two hours, after which point the treatments were removed from all units to avoid habituation. Recordings were downloaded daily and stored on a portable hard drive until they could be extracted and transferred onto a Mac desktop computer for later viewing.

Documenting the behaviors of each pair involved using an instantaneous scan sampling at one-minute time intervals. Documentation of a pair began when at least one subject started to interact with their bowls/feeding enrichment devices. Hence, a single sample contained 121 documented behaviors exhibited by each subject in a pair throughout a morning session. Accordingly, the number of times a subject exhibited a particular behavior within a session was calculated for every sample. Some of the morning session recordings dropped due to human error. Behavioral observations were not recorded for two days during the experimental phase because of late food deliveries. Therefore, behavioral data were collected from 122 viable morning session recordings (244 observational hours).

Behavioral Data Analysis

For each pair, generalized linear mixed models (GLMMs) were used to analyze the impact of phase (fixed factor) on the occurrence of individual behaviors. The unbalanced repeated measures design plus the missing behavioral data points exhibited within each pair were taken into account when running GLMMs. Since the behavioral data were calculated into discrete count data, each GLMM was fitted with either Poisson or negative binomial distributions. If overdispersion occurred in a count data set, then a GLMM used negative binomial distribution. Moreover, zeroinflation was included in a GLMM if a count data set contained more zeros than expected. To account for the different phase comparisons, the output of a GLMM was converted to an analysis of variance output via the calculation of a Wald chi-square test.

Detection of significant differences among the phases within a pair of a particular behavior resulted in the use of a post hoc Tukey test to determine which phases significantly differed from each other. Furthermore, a Wilcoxon rank-sum test was used to determine if significant difference between two phases of the ground pair significantly differs from the suspensory pair. Normalization (via subtraction) of the count data occurred before running Wilcoxon rank-sum tests. This behavioral data analysis was carried out using R (version 4.0.2, RStudio Team, 2020).

Results

Results are focused on the occurrence of the following behaviors: device interaction, exploration, foraging, locomotion, positive interaction, self-grooming, resting, and stereotypic behavior. The behavioral impact of phase (fixed factor) within each pair is presented in Tables III, VI, and IX. If significant differences occurred among the phases within a pair for a particular behavior, then the comparisons between phases (i.e., pre-observational, experimental, & post-observational) regarding the pair's behavior are presented in Tables IV, VII, and X. Only four behaviors (i.e., device interaction, foraging, self-grooming, & stereotypic behavior) required further analysis to determine if the significant difference between two phases of the ground pair significantly differs from the suspensory pair. Altogether, these results were summarized into a simple checklist that shows whether a particular behavior experienced any form of impact from the ground or suspensory feeding enrichment devices (Table XIII).

Device Interaction

Phase significantly impacted the occurrence of device interaction for the control pair, X^2 (2, N = 70) = 8.94, p = 0.01; ground pair, X^2 (2, N = 86) = 54.61, p < 0.001; and suspensory pair, X^2 (2, N = 88) = 14.23, p < 0.001. The control pair interacted with the metal bowl significantly more during the post-observational phase than the pre-observational phase, z = -2.98, p = 0.008 (Table V & Figure II). There was no significant difference between the experimental phase (metal bowl) and pre-observational phase or post-observational phase (Table IV, Table V, & Figure II). The ground pair interacted with the ground feeding enrichment device (experimental phase) significantly more than the metal bowl they received during the pre-observational phase, z = -6.90, p < 0.001 and post-observational phase, z = -4.28, p < 0.001 (Table V & Figure II). Additionally, the pair interacted with the metal bowl significantly more during the post-observational phase than the pre-observational phase, z = -3.04, p = 0.006 (Table V & Figure II). The suspensory pair interacted with the suspensory feeding enrichment device (experimental phase) significantly more than the metal bowl they received during the pre-observational phase, z = -3.75, p < 0.001 (Table V & Figure II). Device interaction did not significantly differ between the post-observational phase (metal bowl) and experimental phase or pre-observational phase (Table IV, Table V, & Figure II). The significant increase in the occurrence of device interaction from the pre-observational phase to the experimental phase for the ground pair was significantly greater than the suspensory pair, W = 1360, p < 0.001 (Table XII).

Natural Active Behaviors

Exploration

Phase did not significantly impact the occurrence of exploration for either the control pair, X^2 (2, N = 70) = 2.02, p = 0.36 or suspensory pair, X^2 (2, N = 88) = 1.61, p = 0.45 (Figure II). Despite that, it did significantly impact the ground pair, X^2 (2, N = 86) = 13.67, p = 0.001. The ground pair explored significantly more during the pre-observational phase than the experimental phase, $z = 3.69$, $p < 0.001$ (Table V & Figure II). Exploration did not significantly differ between the post-observational phase and experimental phase or pre-observational phase (Table IV, Table V, & Figure II).

Foraging

Phase did not significantly impact the occurrence of foraging for the control pair, X^2 (2, $N = 70$) = 4.65, $p = 0.10$ (Figure II). Conversely, it did significantly impact both the ground pair, X^2 (2, $N = 86$) = 30.68, $p < 0.001$ and suspensory pair, X^2 (2, $N = 88$) = 21.51, $p < 0.001$. The ground pair foraged significantly more during the experimental phase than either the pre-observational phase, $z = -2.65$, $p = 0.02$ or post-observational phase, $z = -5.27$, $p < 0.001$ (Table V & Figure II). Moreover, foraging occurred significantly more during the pre-observational phase than the post-observational phase, $z = 2.49$, $p = 0.03$ (Table V & Figure II). The suspensory pair foraged significantly more during the experimental phase than either the pre-observational phase, $z = -4.06$, $p < 0.001$ or post-observational phase, $z = -3.14$, $p = 0.004$ (Table V & Figure II). Foraging did not significantly differ between the pre-observational phase and post-observational phase (Table IV, Table V, & Figure II). The significant increase in the occurrence of foraging from the pre-observational phase to the experimental phase for the ground pair did not significantly differ from the suspensory pair, $W = 711$, $p = 0.07$. Nonetheless, the significant decrease from the experimental phase to the post-observational phase for the ground pair was significantly greater than the suspensory pair, $W = 185$, $p = 0.03$ (Table XII).

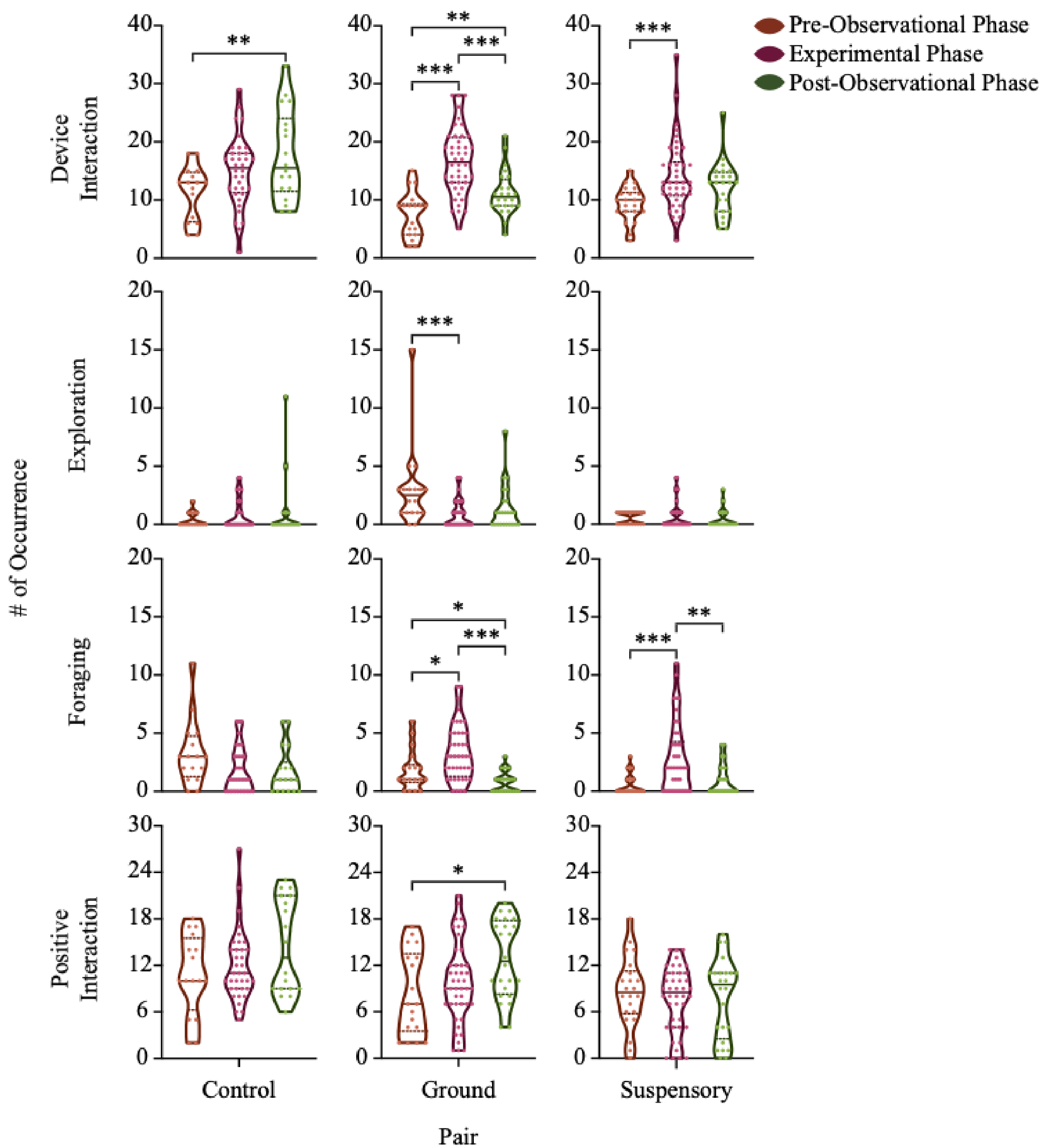

Figure II. The impact of phases on four desirable behaviors within each pair. Individual occurrences of these behaviors are represented as dots. Asterisks and solids lines indicate significant differences between two phases. Median and interquartile range are depicted.

Locomotion

There was no significant impact of phase on the occurrence of locomotion for either the control pair, X^2 (2, N = 70) = 0.89, p = 0.64; ground pair, X^2 (2, N = 86) = 3.91, p = 0.14; or suspensory pair X^2 (2, N = 88) = 1.19, p = 0.55.

Positive Interaction

Phase did not significantly impact the occurrence of positive interaction for either the control pair, X^2 (2, N = 70) = 4.53, p = 0.10 or suspensory pair, X^2 (2, N = 88) = 0.16, p = 0.92 (Figure II). Regardless, it did significantly impact the ground pair, X^2 (2, N = 86) = 7.03, p = 0.03. The ground pair engaged in positive interaction significantly more during the post-observational phase than the pre-observational phase, z = -2.51, p= 0.03 (Table V & Figure II). Positive interaction did not significantly differ between the experimental phase and pre-observational phase or post-observational phase (Table IV, Table V, & Figure II).

Self-Grooming

Phase significantly impacted the occurrence of self-grooming for the control pair, X^2 (2, N = 70) = 6.90, p = 0.03; ground pair, X^2 (2, N = 86) = 15.69, p < 0.001; and suspensory pair, X^2 (2, N = 88) = 14.45, p < 0.001. However, there were no significant differences indicated between any two phases for the control pair (Table VII, Table VIII, & Figure III). The ground pair self-groomed significantly more during the experimental phase than the pre-observational phase, z = -3.75, p < 0.001 (Table VIII & Figure III). Self-grooming did not significant differ between the post-observational phase and experimental phase or pre-observational phase (Table VII, Table VIII, & Figure III). Similarly, the suspensory pair self-groomed significantly more during the experimental phase than the pre-observational phase, z = -3.70, p < 0.001 (Table VIII & Figure III). There was no significant difference between the post-observational phase and experimental phase or pre-observational phase (Table VII, Table VIII, & Figure III). The significant increase in the occurrence of self-grooming from pre-observational phase to experimental phase for the ground pair did not significantly differ from the suspensory pair, $W = 1003$, $p = 0.50$.

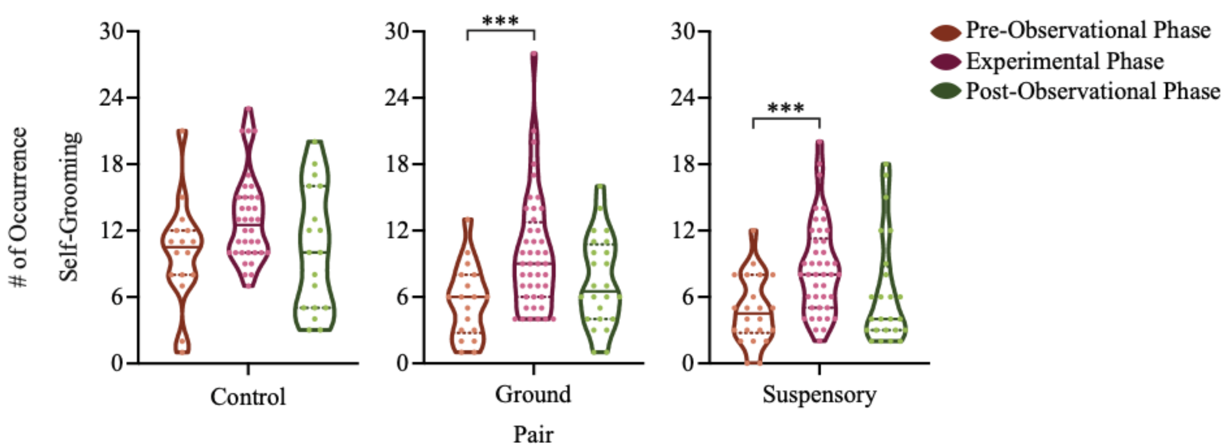

Figure III. The impact of phases on self-grooming within each pair. Individual occurrences of this behavior are represented as dots. Asterisks and solids lines indicate significant differences between two phases. Median and interquartile range are depicted.

Undesirable Behaviors

Resting

Phase did not significantly impact the occurrence of resting for either the control pair, X^2 (2, N = 70) = 1.02, $p = 0.60$ or suspensory pair, X^2 (2, N = 88) = 5.82, $p = 0.05$ (Figure IV). Instead, it did significantly impact the ground pair, X^2 (2, N = 86) = 21.45, $p < 0.001$. The ground pair rested significantly less during the experimental phase than either the pre-observational phase, $z = 3.69$, $p < 0.001$ or post-observational phase, $z = 3.89$, $p < 0.001$ (Table XI & Figure IV). There was no significant difference between the pre-observational phase and post-observational phase (Table X, Table XI, & Figure IV).

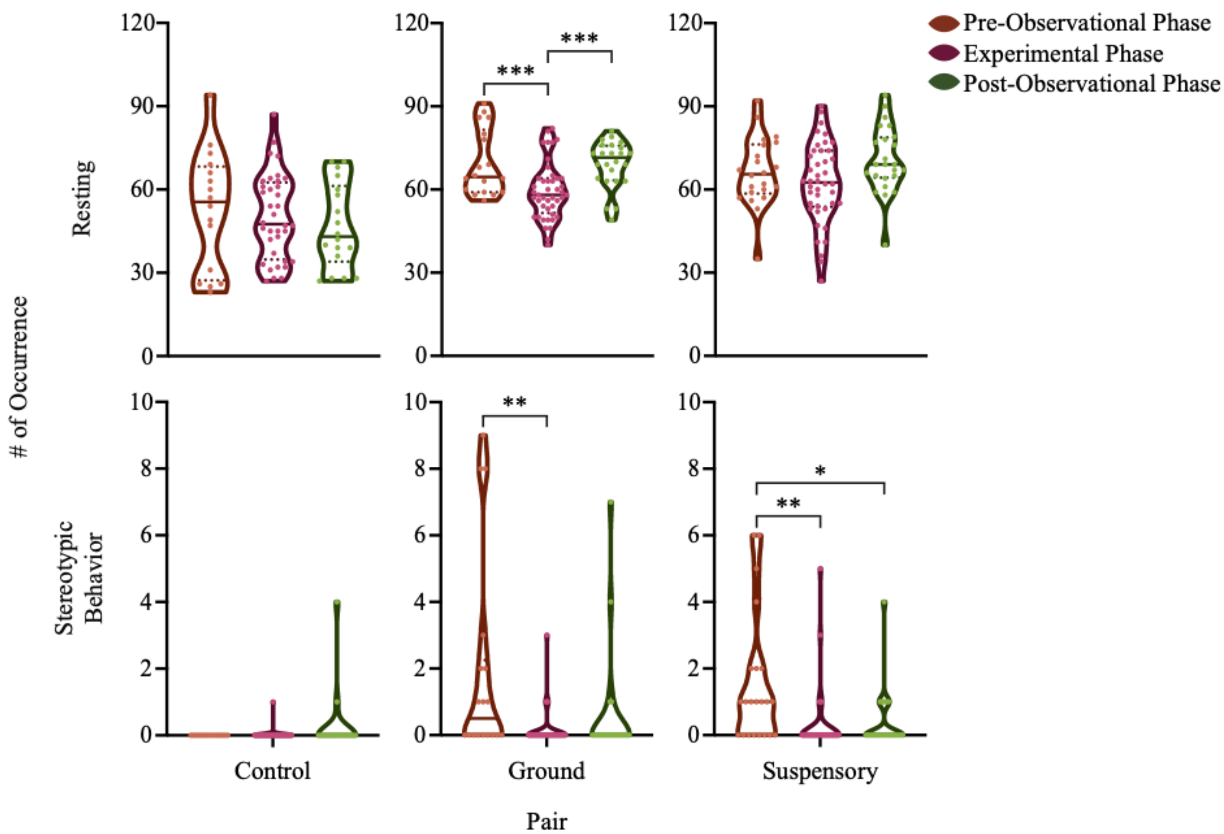

Figure IV. The impact of phases on undesirable behaviors within each pair. Individual occurrences of these behaviors are represented as dots. Asterisks and solids lines indicate significant differences between two phases. Median and interquartile range are depicted.

Stereotypic Behavior

Phase did not significantly impact the occurrence of stereotypic behavior for the control pair, X^2 (2, N = 70) = 4.42, p = 0.11 (Figure IV). Nevertheless, it did significantly impact both the ground pair, X^2 (2, N = 86) = 12.85, p = 0.002 and suspensory pair, X^2 (2, N = 88) = 13.75, p = 0.001. The ground pair engaged in stereotypic behavior significantly less during the experimental phase than the pre-observational phase, z = 3.58, p = 0.001 (Table XI & Figure IV). Stereotypic behavior did not significantly differ between the post-observational phase and experimental phase or pre-observational phase (Table X, Table XI, & Figure IV). The suspensory pair engaged in stereotypic behavior significantly less during the experimental phase than the pre-observational phase, $z = 3.52$, $p = 0.001$ (Table XI & Figure IV). In addition, stereotypic behavior occurred significantly less during the post-observational phase than the pre-observational phase, $z = 2.54$, $p = 0.03$ (Table XI & Figure IV). There was no significant difference between the experimental phase and post-observational phase (Table X, Table XI, & Figure IV). The significant decrease in the occurrence of stereotypic behavior from pre-observational phase to the experimental phase for the ground did not significantly differ from the suspensory pair, $W = 920$, $p = 0.98$.

Discussion

Overall, this study aimed to investigate the impact of two forms of feeding enrichment on the behavior of captive ex-pet ring-tailed lemurs. I hypothesized that presenting their morning diets inside feeding enrichment devices would significantly impact their behavior. Specifically, I predicted that device interaction and natural active behaviors (i.e., exploration, foraging, locomotion, & positive interaction) would increase while undesirable behaviors (i.e., resting & stereotypic behavior) would decrease. Additionally, I hypothesized that a ground feeding enrichment device would have a greater behavioral impact than a suspensory feeding enrichment device. In other words, I predicted that a ground feeding enrichment device would encourage more device interaction, promote more natural active behaviors, and reduce more undesirable behaviors. As expected, my results indicated significant impacts of both feeding enrichment devices on ring-tailed lemur behavior.

Device Interaction

When offered one of the two feeding enrichment devices after the metal bowl, device interaction significantly increased in a pair. Unlike the metal bowl, retrieving food from either of the feeding enrichment devices required more physical effort (e.g., climbing on the ground feeding enrichment device). Nonetheless, the ground feeding enrichment device had a greater effect on this behavior than the suspensory feeding enrichment device. Device interaction significantly decreased once the metal bowl replaced the ground feeding enrichment device. However, the ground pair engaged in this behavior more when offered the metal bowl after the feeding enrichment device than before. In other words, the effectiveness of the ground feeding enrichment device on this behavior produced a significant lasting effect in its pair. Since ring-tailed lemurs are semi-terrestrial (Gould, 2006), the differences between the impact of both forms of feeding enrichment devices on device interaction may be related to their locomotor patterns.

Unexpectedly, device interaction occurred significantly more during the post-observational phase than the pre-observational phase in the control pair. The lack of interaction with the metal bowl during the pre-observational phase may be related to the additional ring-tailed lemur temporarily housed with the pair throughout the first week of the study. Possibly, the control pair was not able to acclimate to the additional ring-tailed lemur and resulted in them being slightly hesitant to retrieve their food. Device interaction was the only behavior in which a significant difference was indicated in the control pair.

Natural Active Behaviors

Exploration significantly decreased in the ground pair when they received their feeding enrichment device after the metal bowl, likely because of their increased interest in their enrichment device. On the other hand, exploration remained the same throughout the study for the suspensory pair. Despite the pair's increased interest in the suspensory feeding enrichment device, it was not as strong as the ground pair's interest to deter exploration.

Foraging significantly increased in the ground and suspensory pairs as each pair received their feeding enrichment device after the metal bowl. The increase of this behavior in the ground pair did not greatly differ from the suspensory pair. The ground feeding enrichment device likely encouraged its pair to spend more time on the ground; therefore, increasing the chances of foraging occurring. Meanwhile, the suspensory pair's food probably fell to the ground when retrieving it from their feeding enrichment device, which resulted in them foraging for their food. Foraging significantly decreased in the ground and suspensory pairs when offered the metal bowl again. The simplicity of the metal bowl might not have been engaging enough as the feeding enrichment devices to encourage foraging. The decrease of this behavior in the ground pair was greater than the suspensory pair. Moreover, the ground pair foraged less when offered the metal bowl after the feeding enrichment device than before.

Positive interaction occurred significantly more when the metal bowl was offered after the ground feeding enrichment device than before. Although this feeding enrichment device did not directly affect this behavior, it possibly generated an after-effect. The suspensory pair did not experience any impact on this behavior throughout the study. Lastly, the only natural active behavior exhibited by both the ground and suspensory pairs that did not experience any impact throughout the study was locomotion.

Self-Grooming

Inadvertently, self-grooming significantly increased in the ground and suspensory pairs as each received their feeding enrichment device after the metal bowl. The increase of this behavior in the ground pair did not greatly differ from the suspensory pair. Both pairs had to insert their hands/mouths into their feeding enrichment device to retrieve their food, which possibly resulted in them getting the juices of the fruits and vegetables on their fur.

Undesirable Behaviors

Resting significantly decreased in the ground pair when they received their feeding enrichment device after the metal bowl. The pair's increased interest in the ground feeding enrichment device likely contributed to the decrease of this behavior. The replacement of the ground feeding enrichment device with the metal bowl resulted in this behavior significantly increasing in the pair. Conversely, resting remained the same throughout the study for the suspensory pair. Although this pair had an increased interest in the suspensory feeding enrichment device, it was not as strong as the ground pair to discourage resting.

Stereotypic behavior significantly decreased in the ground and suspensory pairs as each received their feeding enrichment device after the metal bowl. The decrease of this behavior in the ground pair did not greatly differ from the suspensory pair. Both pairs' increased interest in their feeding enrichment devices probably contributed to the decrease of this behavior. Nonetheless, the suspensory pair engaged in this behavior more when offered the metal bowls after the feeding enrichment device than before. To put it differently, the effectiveness of the suspensory feeding enrichment device on this behavior produced a significant lasting effect in its pair.

Conclusion

The findings of this study emphasized the importance of feeding enrichment as a tool in fostering desirable behaviors while diminishing undesirable ones in captive ring-tailed lemurs. Although a couple of behaviors (i.e., exploration & locomotion) did not support either of the two hypotheses, the majority did. Notably, the findings for device interaction demonstrated that feeding enrichment are more likely to strike a lemur species curiosity, especially those tailored to the distinct behaviors of the species, than a basic food bowl. This increase curiosity exhibited by the suspensory pair discouraged the occurrence of stereotypic behavior. However, the ground feeding enrichment elicited a greater effect in enticing its pair, which most likely lead to the decline in both resting and stereotypic behavior. These undesirable behaviors are commonly observed in illegal pet lemurs caused by poor captive conditions. Pet lemurs often lead isolated lives in small-scale cages that barely provide enough space for them to engage in various natural active behaviors (Reuter & Schaefer, 2016). Providing enrichments that require and encourage natural active behaviors similar to the ones observed in this study (i.e., foraging & positive interactions) is beneficial for the welfare of captive species, especially for those who need rehabilitation. Future studies should further investigate the connection between enrichment effectiveness and the distinct natural behaviors of a species. Research dedicated to husbandry practices, such as environmental enrichment, is needed to enhance and maintain the quality of care for species in captivity.

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Appendix

Table II. Ethogram

Behavior	Definition
Aggressive interaction (AI)	Aggressive behavior displayed toward an individual or between two individuals, including swatting, biting, grabbing, and stink fighting behaviors (Shapiro et al., 2018).
Device interaction (DI)	Manipulating, exploring, or scent marking the feeding devices as well as consuming food from them (Shapiro et al., 2018).
Eating (E)	Food is either licked, placed in one's mouth, or chewed without physically interacting with the feeding devices.
Exploration (EX)	Licking, biting, sniffing, or manipulating the enclosure or objects within, except for the feeding devices (Shapiro et al., 2018).
Foraging (F)	Searching for food in the enclosure either by actively moving through the enclosure or visually searching for it. Also, it included manipulation and sniffing of food without placing it in one's mouth (Baker et al., 2018).
Locomotion (L)	Quadrupedal motion, climbing, or leaping (Shapiro et al., 2018).
Not visible (NV)	Unable to see either the individual or the behavior being displayed by the individual.
Other (O)	Any behavior not described in this ethogram (Shapiro et al., 2018).
Positive interaction (PI)	Non-aggressive behavior displayed toward an individual or between two individuals, including allo-grooming, mutual grooming, and play (Shapiro et al., 2018).
Resting (R)	Inactive (sitting, laying, standing, or hanging), huddling, sleeping, or sunning (Maloney et al., 2006).
Scent marking (SM)	Using scent glands to mark the enclosure or objects within, except for the feeding devices (Shapiro et al., 2018).
Self-grooming (SG)	Using hands, feet, tongue, tooth comb, or grooming claw to itch or clean one's body (Shapiro et al., 2018).

Stereotypic behavior (SB)	Repetitive behaviors, including the same pattern of movement, displayed for no particular purpose (Shapiro et al., 2018).

This ethogram is composed of the behaviors observed during this study, along with their abbreviations and definitions. Occasionally the ring-tailed lemur would display two behaviors simultaneously. The decisions of how to record these occurrences followed: a) Eating superseded locomotion and foraging; b) Self-grooming superseded allo-grooming (Shapiro et al., 2018).

Table III. Impact of phase on the occurrence of desirable behaviors within each pair

Behavior	Pair	Df	N	X^2	Pr ($>X^2$)
Device interaction					
	Control	2	70	8.94	0.01*
	Ground	2	86	54.61	< 0.001***
	Suspensory	2	88	14.23	< 0.001***
Exploration					
	Control	2	70	2.02	0.36
	Ground	2	86	13.67	0.001**
	Suspensory	2	88	1.61	0.45
Foraging					
	Control	2	70	4.65	0.10
	Ground	2	86	30.68	< 0.001***
	Suspensory	2	88	21.51	< 0.001***
Locomotion					
	Control	2	70	0.89	0.64
	Ground	2	86	3.91	0.14
	Suspensory	2	88	1.19	0.55
Positive interaction					
	Control	2	70	4.53	0.10
	Ground	2	86	7.03	0.03*
	Suspensory	2	88	0.16	0.92

*$p < 0.05$
**$p < 0.01$
***$p < 0.001$

Table IV. Comparisons between phases within a pair for four desirable behaviors

Behavior	Pair	Phase A	Phase B	z value	Pr (>|z|)
Device interaction					
	Control	Pre	Exp	-2.08	0.09
		Exp	Post	1.38	0.35
		Post	Pre	-2.98	0.008**
	Ground	Pre	Exp	-6.90	< 0.001***
		Exp	Post	-4.28	< 0.001***
		Post	Pre	-3.04	0.006**
	Suspensory	Pre	Exp	-3.75	< 0.001***
		Exp	Post	-1.57	0.26
		Post	Pre	-2.04	0.10
Exploration					
	Ground	Pre	Exp	3.69	< 0.001***
		Exp	Post	1.37	0.36
		Post	Pre	2.14	0.08
Foraging					
	Ground	Pre	Exp	-2.65	0.02*
		Exp	Post	-5.27	< 0.001***
		Post	Pre	2.49	0.03*
	Suspensory	Pre	Exp	-4.06	< 0.001***
		Exp	Post	-3.14	0.004**
		Post	Pre	-1.17	0.47
Positive interaction					
	Ground	Pre	Exp	-1.00	0.57
		Exp	Post	2.00	0.11
		Post	Pre	-2.51	0.03*

*$p < 0.05$
**$p < 0.01$
***$p < 0.001$

Table V. Median and interquartile range (IQR) of phases within each pair for four desirable behaviors

Behavior	Pair	Phase	Median	IQR
Device interaction				
	Control	Pre	13.00	6.75 to 14.25
		Exp	15.50	11.75 to 18.00
		Post	15.50	12.00 to 22.75
	Ground	Pre	9.00	4.25 to 9.00
		Exp	16.50	13.00 to 20.25
		Post	10.50	9.00 to 12.50
	Suspensory	Pre	10.00	8.00 to 11.00
		Exp	13.00	11.00 to 16.00
		Post	13.00	8.00 to 14.25
Exploration				
	Control	Pre	0.00	0.00 to 1.00
		Exp	0.00	0.00 to 1.25
		Post	0.00	0.00 to 0.75
	Ground	Pre	2.50	1.00 to 3.00
		Exp	0.00	0.00 to 1.25
		Post	1.00	0.00 to 2.00
	Suspensory	Pre	0.50	0.00 to 1.00
		Exp	0.00	0.00 to 1.00
		Post	0.00	0.00 to 1.00
Foraging				
	Control	Pre	3.00	1.75 to 4.25
		Exp	1.00	0.00 to 3.00
		Post	1.00	0.00 to 2.00
	Ground	Pre	1.00	1.00 to 2.00
		Exp	3.00	1.75 to 5.00
		Post	1.00	0.00 to 1.00
	Suspensory	Pre	0.00	0.00 to 1.00
		Exp	2.00	0.00 to 4.00
		Post	0.00	0.00 to 2.00
Positive interaction				
	Control	Pre	10.00	8.75 to 14.50
		Exp	11.00	9.00 to 14.00
		Post	13.00	9.00 to 20.75

	Ground	Pre	7.00	4.00 to 13.00
		Exp	9.00	7.00 to 12.00
		Post	12.50	8.75 to 17.25
	Suspensory	Pre	8.50	6.00 to 10.75
		Exp	8.50	4.25 to 11.00
		Post	9.50	3.50 to 11.00

Table VI. Impact of phase on the occurrence of self-grooming within each pair

Behavior	**Pair**	**Df**	**N**	**X^2**	**Pr (>X^2)**
Self-grooming					
	Control	2	70	6.90	0.03*
	Ground	2	86	15.69	< 0.001***
	Suspensory	2	88	14.45	< 0.001***

*p < 0.05
**p < 0.01
***p < 0.001

Table VII. Comparisons between phases within each pair for self-grooming

Behavior	Pair	Phase A	Phase B	z value	Pr (>|z|)
Self-grooming					
	Control	Pre	Exp	-2.15	0.08
		Exp	Post	-2.07	0.10
		Post	Pre	-0.16	0.99
	Ground	Pre	Exp	-3.75	< 0.001***
		Exp	Post	-2.26	0.06
		Post	Pre	-1.61	0.23
	Suspensory	Pre	Exp	-3.70	< 0.001***
		Exp	Post	-1.99	0.11
		Post	Pre	-1.64	0.23

*$p < 0.05$
**$p < 0.01$
***$p < 0.001$

Table VIII. Median and interquartile range (IQR) of phases within each pair for self-grooming

Behavior	Pair	Phase	Median	IQR
Self-grooming				
	Control	Pre	10.50	8.00 to 12.00
		Exp	12.50	10.00 to 15.00
		Post	10.00	5.00 to 15.25
	Ground	Pre	6.00	3.00 to 7.75
		Exp	9.00	6.00 to 12.25
		Post	6.50	4.00 to 10.25
	Suspensory	Pre	4.50	3.00 to 7.50
		Exp	8.00	5.25 to 11.00
		Post	4.00	3.00 to 8.25

Table IX. Impact of phase on the occurrence of undesirable behaviors within each pair

Behavior	Pair	Df	N	X^2	Pr ($>X^2$)
Resting					
	Control	2	70	1.02	0.60
	Ground	2	86	21.45	< 0.001***
	Suspensory	2	88	5.82	0.05
Stereotypic behavior					
	Control	2	70	4.42	0.11
	Ground	2	86	12.85	0.002**
	Suspensory	2	88	13.75	0.001**

*$p < 0.05$
**$p < 0.01$
***$p < 0.001$

Table X. Comparisons between phases within a pair for undesirable behaviors

Behavior	Pair	Phase A	Phase B	z value	Pr (>|z|)
Resting					
	Ground	Pre	Exp	3.69	< 0.001***
		Exp	Post	3.89	< 0.001***
		Post	Pre	0.13	0.99
Stereotypic behavior					
	Ground	Pre	Exp	3.58	0.001**
		Exp	Post	1.89	0.14
		Post	Pre	1.73	0.19
	Suspensory	Pre	Exp	3.52	0.001**
		Exp	Post	0.63	0.81
		Post	Pre	2.54	0.03*

*$p < 0.05$
**$p < 0.01$
***$p < 0.001$

Table XI. Median and interquartile range (IQR) of phases within each pair for undesirable behaviors

Behavior	Pair	Phase	Median	IQR
Resting				
	Control	Pre	55.50	29.75 to 66.75
		Exp	47.50	36.25 to 61.50
		Post	43.00	36.75 to 59.50
	Ground	Pre	64.50	59.25 to 79.50
		Exp	58.00	52.50 to 64.00
		Post	71.50	63.75 to 75.25
	Suspensory	Pre	65.50	59.25 to 75.00
		Exp	62.50	54.25 to 73.50
		Post	69.00	64.75 to 78.25
Stereotypic behavior				
	Control	Pre	0.00	0.00 to 0.00
		Exp	0.00	0.00 to 0.00
		Post	0.00	0.00 to 0.00
	Ground	Pre	0.50	0.00 to 2.00
		Exp	0.00	0.00 to 0.00
		Post	0.00	0.00 to 0.00
	Suspensory	Pre	1.00	0.00 to 2.00
		Exp	0.00	0.00 to 0.00
		Post	0.00	0.00 to 0.25

Table XII. Median and interquartile range (IQR) of the ground and suspensory pairs for two desirable behaviors

Behavior	Pair	Median	IQR
Device interaction			
	Ground	8.50	5.67 to 12.47
	Suspensory	3.45	1.45 to 6.73
Foraging			
	Ground	-2.55	-3.34 to -1.55
	Suspensory	-1.29	-2.73 to -1.29

Table XIII. Checklist

Behavior	**Ground Feeding Enrichment**	**Suspensory Feeding Enrichment**
Device interaction	✓ (red)	✓
Exploration	✓	
Foraging	✓	✓
Locomotion		
Positive interaction	✓	
Resting	✓	
Self-grooming	✓	✓
Stereotypic behavior	✓	✓

The checkmark signifies that the feeding enrichment device either directly or indirectly impacted a behavior. The red checkmark indicates that the ground feeding enrichment device had a greater direct impact on device interaction than the suspensory feeding enrichment device.