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RESEARCH ARTICLE

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Material and food exploration by zoo-housed animals can inform cognition and enrichment apparatus design

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Abstract

To robustly study zoo animal cognition and provide effective enrichment, we must provide animals with carefully designed apparatus made from appropriate (safe, attractive, practical) materials. However, all too often, this design phase is overlooked or omitted from the literature. We evaluated how a troop of 12 ring-tailed lemurs (*Lemur catta*) explored a range of novel materials and whole foods during outdoor social testing. These items were not intended to test cognition or be enriching; rather we viewed them as the potential "building blocks" from which to build our future apparatus. Lemurs preferred to explore wooden surfaces, but had no preference for manipulanda made from different materials. Large amounts of metal and untreated wood should be avoided in the future; metal produced too much heat and glare, and wood was damaged by biting/chewing. Lemurs used one or two hands to explore manipulanda, and simple touching was more common than twisting or pulling. However, lemurs were most likely to explore by smell than touch or by mouth. Social testing preserved "normal" conditions for the lemurs, including natural food stealing and scrounging in high- and low-ranking individuals, respectively. Our findings culminated in the development of a static, low-level cognitive task apparatus, constructed from modular plastic units. We encourage other researchers to report how they develop cognitive and enrichment apparatuses and consider a similar preference-testing approach.

KEYWORDS

animal cognition, enrichment, investigation, *Lemur catta*, novelty, preference test

1 | INTRODUCTION

As zoos continue to evolve their scientific activities, zoo-based cognitive research is increasing (Hopper, 2017; Garcia-Pelgrin et al., 2022; MacDonald & Ritvo, 2018), and we hold enrichment to increasingly rigorous standards (Riley & Rose, 2020). Animal cognitive skills cannot be observed directly, but we can make inferences from animals' performance on specially designed cognitive tasks (Shaw & Schmelz, 2017; Shettleworth, 2010; Thornton et al., 2014). The Wisconsin General Test Apparatus (WGTA) and other traditional apparatuses (i.e., specific, structural equipment) have been popular for many decades but were designed for animals under highly-controlled conditions. For zoo-based cognition research to flourish, we must develop new cognitive tasks suitable for less controlled conditions and group testing (Vonk, 2016). Cognitive testing can be enriching (Clark, 2017; Herrelko et al., 2012; Perdue et al., 2012) and vice versa; cognitively challenging enrichment can provide knowledge about cognitive skills (Clark et al., 2019; Matrai et al., 2020).

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Therefore, there are many benefits to designing effective, safe, attractive, and practical apparatuses for zoo animals.

A variety of "pure" (i.e., not enrichment-related) cognitive tasks have been constructed for lemurs (e.g., wooden boxes with hinged lids, vs. transparent acrylic puzzle boxes with sliding mechanisms; see Kittler et al., 2015, for a review of ring-tailed lemurs, *Lemur catta*) with very little justification for the design features or construction materials used (*Lemur*: Fornasieri et al., 1990; Kappeler, 1987; Kendal et al., 2010; *Eulemur*: Genty et al., 2004; Huebner & Fichtel, 2015; Schnoell & Fichtel, 2012; *Propithecus*: Rushmore et al., 2012; *Varecia:* Dean et al., 2011; Stoinski et al., 2011). There is also a lack of information on how naïve lemurs with no previous training or habituation to tasks respond; cognitive studies very often involve an undocumented "familiarization" or pilot phase.

We propose that preference testing should inform apparatus design (for cognition research, enrichment, or both). Preference testing has been commonplace since the 1970s to establish animals' relative preferences for different diets, bedding materials, commercial enrichment items, and other management variables (Fraser & Nicol, 2011; Kirkden & Pajor, 2006). It seems logical, therefore, that preference testing can be used to select appropriate "building blocks" or raw materials from which to build new apparatuses, as well as explore how animals prefer to explore materials. Fernandez and Timberlake (2019) used preference testing to assess different food items for ring-tailed lemurs, but to our knowledge similar procedures have not been undertaken on raw materials. Some recent studies have evaluated the behavioral responses of ring-tailed lemurs to a variety of enrichment objects (Laméris et al., 2021; Shapiro et al., 2018) but there is no clear understanding of how the design features or materials contribute to enrichment success.

The current study aimed to explore the responses of a troop of 12 socially-housed ring-tailed lemurs to materials and foods. These items were not intended to test cognition or be enriching; rather we viewed them as the potential "building blocks" from which to build our future apparatus. We presented different *surfaces* (i.e., candidate materials to build the main framework structure of an apparatus) and *manipulanda* (i.e., candidate materials to build manipulatable pieces of an apparatus; *sensu* Washburn et al., 2017). Furthermore, we presented different novel whole food items to assess how lemurs may use their different body parts to explore them. The time lemurs spent with each material was used as a general indicator of preference (Fraser & Matthews, 1997). We did not aim to test lemurs' preferences for consuming different foods because it may take them different amounts of time to access the edible parts depending on leaves, shells, and so forth, and we were not interested in choosing a preferred food reward in the current study.

We were interested to see whether lemurs used one or both hands to investigate manipulanda, because using both hands makes it harder to find a comfortable posture and therefore would perhaps confound task use. Finally, we were interested in the effects of social testing because it is a more ecologically relevant condition than lone testing. However, allowing foraging to take place socially means that it is likely to be affected by dominance structure. We predicted high-ranking subjects in our study would have a lower latency to approach materials and foods, whereas low-ranking subjects would adopt a "scrounging" strategy typical of low-ranking lemurs (O'Mara & Hickey, 2012).

The results of this study were used to help design a new cognitive task apparatus suitable for ring-tailed lemurs, as part of the "Lemur Bootcamp" project (established at Bristol Zoological Society and University of Bristol, 2017). Data on *which* materials lemurs preferred to explore, and *how* they explored materials and novel foods (in a social context), was used to justify certain apparatus design features and construction materials (Schubiger et al., 2020). We chose to test lemur responses to raw materials rather than a completed new apparatus or parts thereof; this was to reduce habituation to the final product and ensure lemurs were not inadvertently trained to solve the apparatus through incremental exposures to it.

2 | METHODS

2.1 | Study subjects and housing

The study took place at the Wild Place Project (Bristol, UK) between May 22 and July 24, 2017. Study subjects were a troop of seven adult and five juvenile ring-tailed lemurs (Table 1). This troop's size, demographic structure and housing are typical for ring-tailed lemurs in UK zoos (Species 360, 2018, http://www.zims.species360.org). Lemurs were housed together in an outdoor walk-through enclosure (L 20 m, W 40 m). The enclosure had a winding visitor pathway

TABLE 1 Information on the ring-tailed lemur troop housed at Wild Place Project.

Subject ID	Age (y)	Sex	Birth and rearing	Years at zoo	Offspring
A	9	M	Other	4	Sire of E, F, G, H, I, J, K, L
B	9	F	Other	4	Dam of K, L
C	8	F	Other	4	Dam of E, H
D	5	F	Other	4	Dam of G, I, J
E	4	F	Other	4	
F	4	F	WPP	3	
G	3	F	WPP	3	
H	1	F	WPP	1	
I	1	M	WPP	1	
J	1	F	WPP	1	
K	1	F	WPP	1	
L	1	F	WPP	1	

Note: Subjects sorted by descending age, rounded to the nearest year. Birth and rearing took place at Wild Place Project (WPP) or another zoo (Other). All subjects were mother-reared.

surrounded by trees and other vegetation, wooden platforms and shelters, and climbing frames connected by ropes. A pair of mongoose lemurs (*Eulemur mongoz*) also shared the outdoor enclosure, but not during trials. The indoor enclosure was not used for trials. The feeding schedule consisted of a dried pellet scatter at 08:00 h, and 2.5 kg vegetables (usually broccoli, cabbage, carrot, onion, parsnip, pepper, and sweet potato) roughly chopped and placed on a wooden feeding platform at 11:00, 13:00, and 15:00 h. Water was available ad libitum from water dishes.

2.2 | Ethical review

Lemur's participation in the study was entirely voluntary. The normal diet was unrestricted, and experimental trials were timed to fit with normal management routines. Research passed ethical review by Bristol Zoological Society and the University of Bristol in April 2017 (reference UB/17/020).

2.3 | Novel materials

Four types of materials were presented in this study: metal, plastic, stone, and wood. All forms of material were carefully chosen to avoid any toxic surface treatments (which are commonly applied to construction materials for weather-proofing or pest control), or small holes which might trap fingers or limbs. We tested surfaces (i.e., to construct the framework of the apparatus on which lemurs could bear weight) and manipulanda (i.e., component pieces for lemurs to hold and move).

Surfaces were: (1) aluminum metal sheet with an embossed diamond pattern (Alfer®; Baden-Württemberg); (2) royal blue PVC tile with an embossed square pattern (Coba Europe Ltd.); (3) gray stone tile (unknown origin); and (iv) medium-density fiberboard (MDF). A 100 × 50 cm sheet of each substrate was cable-tied to a small horizontal frame (100 × 50 × 15 cm) made from white PVC pipe (FloPlast Ltd., Figure 1).

Manipulanda were: (1) spherical chrome door knobs, 3 cm diameter (Screwfix Direct Ltd.); (2) fluorescent yellow and pink plastic rock-climbing holds, 10 cm diameter (sourced from a local indoor climbing center); (3) pale gray stone climbing holds, 10 cm diameter (also from the climbing center), and (4) oak tree branches, 12 × 2.5 cm. Six copies of each material were bolted to a sheet of plain MDF (100 × 50 cm) and placed on an A-frame constructed from white PVC plumbing pipe (100 × 50 cm, slanted 75°).

Novel whole foods were: (1) artichoke, (2) butternut squash, (3) coconut, and (4) sweetcorn. These foods were chosen because the lemurs were naïve to them, and they require physical/cognitive work to extract the edible parts. Furthermore, they were in season and relatively low in sugar content (in accordance with Bristol Zoological Society's primate nutrition strategy). Foods were provided in their unprocessed format with the skin, shell or husk intact: artichoke had the petals and stem intact; butternut squash had a tough, contiguous skin and short stem intact; coconut and sweetcorn had full, fibrous husks.

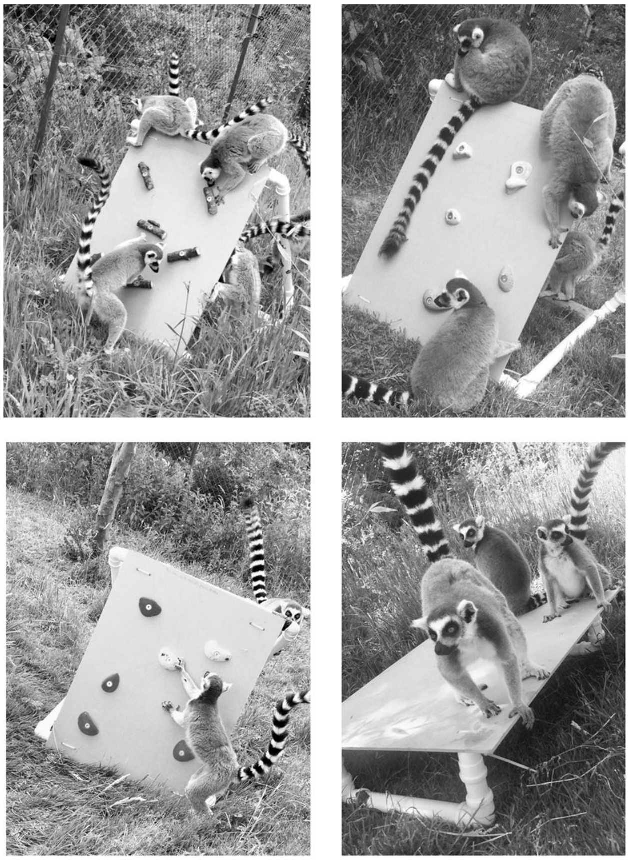

FIGURE 1 Images of some of materials preference-tested on ring-tailed lemurs. Top left: wooden manipulanda. Top right: A-frame with stone manipulanda. Bottom left: plastic manipulanda. Bottom right: wooden surface.

2.4 | Data collection

2.4.1 | Baseline

The group was observed for three sessions of 60 min duration, under normal management, during 1 week in May 2017. Each session was undertaken on a different day beginning at 15:00 h to coincide with the normal afternoon feeding schedule. Empty frames (no materials attached) and dummy camera equipment (not switched on) were placed in the outdoor enclosure so that lemurs could habituate to their presence before experimental trials began. Ring-tailed lemurs have female dominance (Sauther, 1998), so we only calculated a female dominance hierarchy as follows. Agonistic interactions between females were recorded using all-occurrence sampling (Altmann, 1974; Martin & Bateson, 2007) and were summed across the 3 h baseline. These included charges, chases, lunges, bites, nips, and cuffs (Cavigelli et al., 2003) and we did not include food-stealing because this was not deemed to be overly aggressive. Following

Cavigelli et al. (2003), a linear female dominance rank was then determined by putting frequencies of aggression into an interaction matrix then reordering values until the number of aggressive acts below the diagonal was minimized.

2.4.2 | Trials

Trials took place over June and July 2017, on 3 or 4 randomized days per week. However, a trial was rescheduled for the next dry day if rain was forecast. Trials of surfaces, manipulanda, and whole foods took place in randomized order, and never on the same day. Following the pairwise testing procedure of Worth et al. (2015), lemurs were exposed to two surfaces or manipulanda simultaneously. These were placed 5 m apart on flat ground on either side of the visitor pathway in the outdoor enclosure. There were six possible pairings of surfaces (metal + plastic, metal + stone, etc.) and the same for manipulanda, giving rise to six trials of surfaces and six trials of manipulanda. These pairings were randomized without replacement (Lehner, 1998). Trials were 60 min duration and started at either 11:30 or 14:00 h to avoid enclosure cleaning, visitor talks, and the feeding schedule. Two tripod-mounted camcorders (Sony HDR-CX405; Sony Corporation) filmed lemurs within a 0.5 m radius of each frame. Frames and cameras were removed from the enclosure, cleaned with a dry brush, and stored in a shed at the end of each trial. Videos were played back using Windows Media Player® version 10 (Microsoft©) and coded by one observer into Microsoft Excel (2010). Continuous sampling of all subjects within 0.5 m of the frame was coded, and all investigatory behavior was categorized according to an ethogram (Table 2). The duration of time each lemur spent using one or both hands to investigate manipulanda was also calculated from the coded footage. Foot use was excluded from analysis because feet were nearly always used bimanually (i.e., two feet at the same time) to support hand use.

Whole food items were presented in a similar way to surfaces described above, but this time a novel food was always paired with the normal daily diet. The primary goal of whole food presentation was to provide exploration opportunities, not to find the most preferred foods (contrast to Hopper et al., 2018). Animal keeping staff also wanted lemurs to have access to their normal diet at normal feeding times. Each food type was trialed twice alongside the normal diet, giving rise to eight food trials in total, each of 60 min duration. Trials started at 15:00 h to coincide with the afternoon feeding session. During a trial, approximately 2.5 kg of one type of whole food (two whole butternut squash, two whole coconuts, five whole artichokes or two whole sweetcorn) was placed on a wooden feeding platform in the enclosure, and 2.5 kg normal chopped food placed on another platform (as it would normally be during routine feeding). The two feeding platforms were approximately 1.5 m high and spaced 5 m apart. The platform used for each food type was randomized across trials. At the end of a 60 min trial, remnants of whole food were removed from the enclosure and the feeding platform was cleaned with a dry brush. Trials were filmed and coded as described for materials, according to an ethogram (Table 2).

2.5 | Statistical analyses

The total duration of time each lemur spent exploring each material was analyzed as a percentage of time it was accessible. This is because, on a few unforeseen occasions, a lemur could not be included in a trial due to isolation following a group fight. Statistical analyses were undertaken using Statext version 3.0 (Statext LLC). Exploratory data analysis revealed data were not normally distributed, and thus troop-level medians along with interquartile ranges (IQRs) were used for exploratory and confirmatory analyses (Schnoell & Fichtel, 2012).

Lemurs' overall preference for different materials was analyzed by performing tests on troop medians for each pairing of materials. For this purpose, a Skillings–Mack (S-M) test was chosen as a nonparametric, general Friedman-type statistic to compare treatment effects in a block design that has missing data (i.e., some lemurs missing from some trials; Cunningham, 2010; Skillings & Mack, 1981). We considered that p values from the χ^2 approximation may be too conservative for our data (Cunningham, 2010), so p values for S-M tests were simulated using the Monte Carlo method with 20,000 simulations per test. Post hoc pairwise Wilcoxon tests were undertaken where necessary. A threshold significance level of $p \le .05$ was set, except where a Bonferroni adjustment was required to correct for multiple pairwise testing. The types of exploratory behavior (olfactory, tactile, oral) used were compared using the same tests.

Following Bennett et al. (1995), the strength of uni/bi-handedness (i.e., using one or two hands at a time to explore manipulanda) was analyzed per subject by performing binomial tests with a probability set at 0.5. Finally, Spearman's rank tests were run to find if there was a correlation between the linear dominance rank of the 10 females in the troop and: (a) the median and lowest duration of time taken for a lemur to contact a surface, manipulanda or food across all trials and (b) the percentage of time a lemur spent exploring a surface, manipulanda or food across all trials.

3 | RESULTS

3.1 | Exploration of materials

Lemurs spent an average of 32 min (interquartile range [IQR]: 24 min) exploring surfaces summed across six trials (8.9% of 6 h, IQR: 6.7%). There was an overall effect of surface type on exploration (S-M test statistic = 17.660, $p < .001$), and pairwise testing revealed significant differences as follows: wood>metal ($Z = 3.040$, $p < .005$), stone>metal ($Z = 2.645$, $p < .0084$), wood>plastic ($Z = 2.883$, $p < .005$). The overall order of preference for surfaces therefore appeared to be wood > stone > plastic > metal (Figure 2). When exploration was split into different types, there was no overall effect of surface type on olfactory or oral exploration. However, there was an overall effect of surface type on manual exploration (S-M test statistic = 8.409, $p < .05$), and pairwise testing revealed one significant difference: metal > stone ($Z = 2.645$, $p < .0084$).

TABLE 2 Ethogram of investigatory behaviors of ring-tailed lemurs.

Material-directed behavior	Description
Olfactory exploration	
Sniff	The nose is placed in close contact with material, slow movement across the material, nostril movement may be observed.
Scent-mark[a]	*Males*
	Wrist-marking: the antebrachial organ is rubbed across the material to deposit scent secretion. An audible click from the wrist spur may be heard.
	Shoulder-rubbing: the secretions of the antebrachial and brachial organs are mixed by pressing a wrist against the ipsilateral shoulder.
	Males/females
	Genital marking: standing on forelegs to smear the genital gland against the material.
Oral exploration	
Bite/chew[b]	Oral manipulation of material, clamping down with the jaw once or repeatedly, without eating.
Manual exploration	
Touch[b]	Simple touching of material, without manipulating it further. One or both hands/feet.
Pull/twist[b]	Hold on to material with one or both hands/feet, either exerting force so as to cause movement towards oneself, or rotating (the manipulanda) clockwise or anticlockwise around its bolted position.
Passive use	
Rest	Use material to rest upon in various postures such as sit, lie, crouch, stand. Non-social. May be asleep or awake.
Socialize	Use material to rest upon while undertaking social behaviors such as allo-grooming, playing, aggression. Where animal is both resting and socializing, behavior is recorded as socializing.
Food-directed behavior	**Description**
Consume	
Consume	Ingest or manipulate food with the mouth. Includes oral exploration (see description for materials, above).
Investigate	
Handle	Split into olfactory and manual exploration (see descriptions for materials, above).
Transport	Move food item away from its original location, carry a distance more than three body lengths.
Indirectly acquire	
Scrounge[c]	Take food previously discovered by a conspecific, which has been discarded or has fallen.
Steal	Actively take food from the possession of a conspecific.
Other	Other behavior not listed above.
Out of sight	Subject not visible in the outdoor enclosure (is occluded by something, or may be indoors).

[a]Following the descriptions of scent-marking in Scordato and Drea (2007).
[b]Following the definitions of primate manipulation of physical objects in Torigoe (1985).
[c]As per the definition of scrounging in Giraldeau and Lefebvre (1987).

Lemurs explored surfaces most often by sniffing/scenting, followed by manual exploration (touching, twisting, pulling) and least often by oral exploration (biting/chewing, Figure 3). There was a significant difference in the duration time lemurs used different forms of exploration (S-M test statistic = 19.292, $p < .0001$), and pairwise testing revealed significant differences as follows: olfactory > oral ($Z = 3.040$, $p < .017$), manual > oral ($Z = 2.636$, $p < .017$). However, most time within 0.5 m of surfaces was spent passively using them to rest and/or socialize upon (Figure 3).

Lemurs spent an average 5 min (1.4% of 6 h), IQR: 5 min (IQR: 1.4%) exploring manipulanda summed across all trials. There was no overall effect of material type on the duration of exploration ($p > .05$), but the order of preference for manipulanda appeared to be stone > wood > plastic > metal (Figure 2). When exploration was split into different types, there was no overall effect of manipulanda type on oral exploration. However, there was an overall effect of manipulanda type on olfactory exploration (S-M test statistic = 15.7, simulated $p < .05$), and pairwise testing revealed significant pairwise differences: metal > plastic

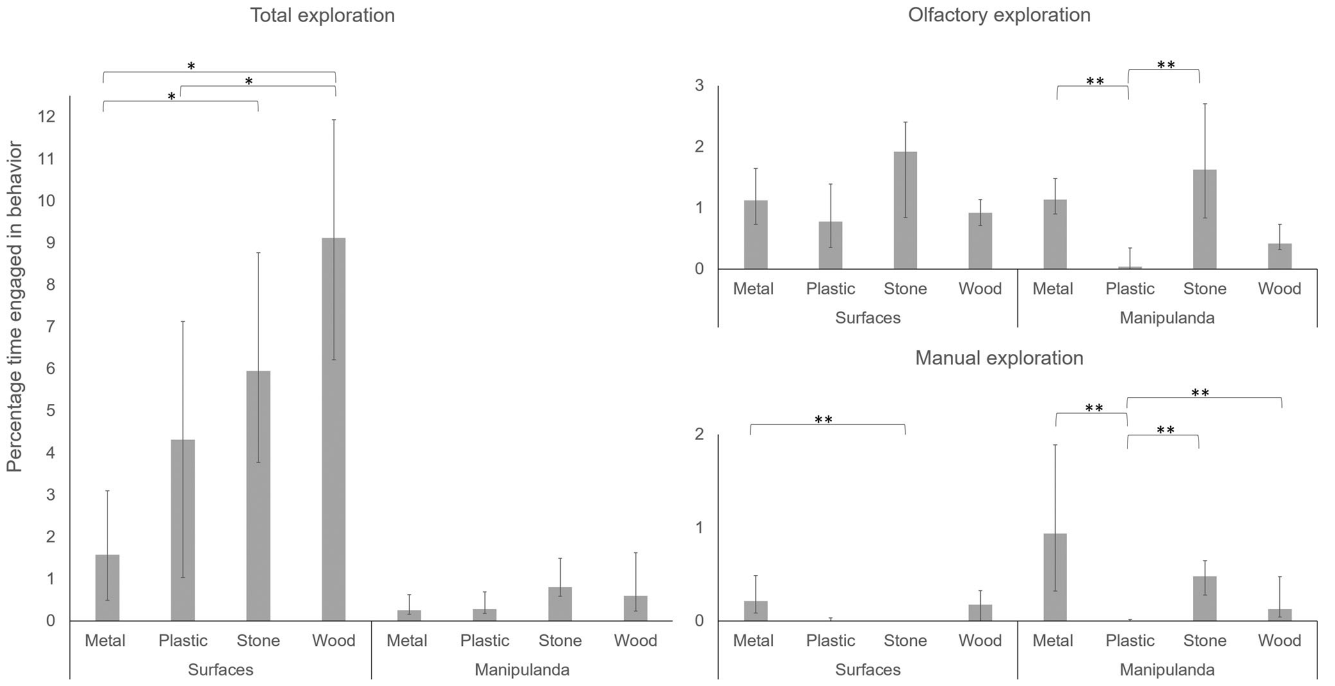

FIGURE 2 Percentage time ring-tailed lemurs spent exploring different surfaces and manipulanda. Troop medians are presented with interquartile ranges. Left: all types of exploration (olfactory, oral, manual) combined. Right: Exploration split into olfactory and manual (data for oral exploration not shown due to negligible values). Significant differences between medians are shown by square brackets. *Significant at $p \le .05$. **Significant at the Bonferroni-adjusted level of $p \le .0084$.

($Z = 2.823$, $p < .0084$), stone > plastic ($Z = 2.491$, $p < .0084$). There was also an overall effect of manipulanda type on manual exploration (S-M test statistic = 21.075, simulated $p < .0001$), and pairwise testing revealed significant pairwise differences: metal > plastic ($Z = 3.040$, $p < .0084$), stone > plastic ($Z = 2.2.912$, $p < .0084$), wood > plastic ($Z = 2.823$, $p < .0084$).

Lemurs most often investigated manipulanda using olfaction, followed by manual exploration and least often by oral exploration (Figure 3). There was a significant difference in the duration time lemurs used different forms of exploration (S-M test statistic = 20.667, simulated $p < .0001$), and pairwise testing revealed significant differences as follows: olfactory>manual ($Z = 2.804$, $p < .017$), olfactory > oral ($Z = 3.040$, $p < .017$), manual > oral ($Z = 3.06$, $p < .017$). Lemurs were very rarely observed biting and chewing manipulanda (median 0.4%–1.6% time), but when this was done to wooden components it caused noticeable damage to the wood (tooth marks, flaking pieces).

Seven out of 12 lemurs were significantly unilateral when exploring manipulanda, meaning that they used one hand significantly more than two hands at a time (Table 3). Their other, nonexploratory hand was used for postural support. Four out of 12 lemurs were significantly bilateral, and one lemur showed no preference for using one hand or two (Table 3).

3.2 | Exploration of whole foods

On average, the troop spent 17 min (IQR: 17 min) exploring (oral/olfactory/manual) any whole food summed across eight trials, which is equivalent to 3.5% (IQR: 3.5%) of the total time accessible. This was compared to a slightly lower median level of 15 min (IQR: 8 min) spent exploring the normal diet, equivalent to 3.1% (IQR: 1.7%).

When lemurs were within 0.5 m of their normal food (on a feeding platform), most of their time (median 80.9%) was spent consuming or orally exploring the food (Figure 4). The whole food items with leaves/husks (artichoke, sweetcorn) were handled and orally investigated/consumed more than the food items with tough outer shells (butternut, coconut), which were subjected to more olfactory exploration. We observed removal of leaves/husks using the mouth and hands, whereas hard-shelled foods were often rolled around on top of a food platform using one or two palms. We did not observe any percussive actions (e.g., striking whole food against a surface, or striking whole food with a hand or object).

3.3 | Effects of social testing

Lemurs nearly always investigated materials socially, that is, within 0.5 m of at least one other lemur (Figure 1). The dominance rank of the 10 females in the troop was calculated from a total of 67 female-female aggressive interactions observed over the 3 h baseline period. The ranking was also corroborated by the keeper's daily reports written within 1 month of the baseline. The order of dominance from most to least was D > G > E > K > L > J > B > H > C > F. Subject D was the dam of the most (three) current offspring in the troop. There were no significant correlations between female dominance rank and the median or lowest latency to contact materials or food, or the

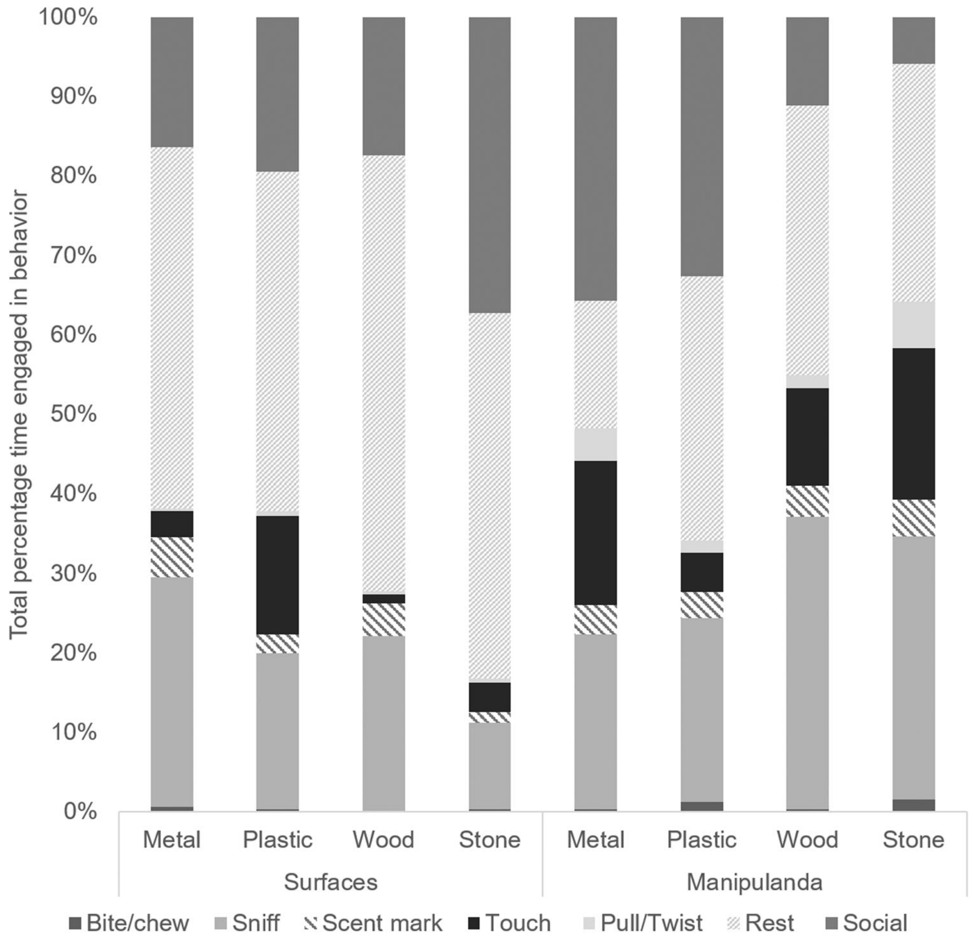

FIGURE 3 Behaviors used by ring-tailed lemurs to investigate or passively use (rest, socialize upon) novel metal, plastic, stone and wood surfaces and manipulanda. Troop medians are presented.

TABLE 3 Uni (one) or bi (two) handedness by ring-tailed lemurs exploring frame-mounted manipulanda.

Subject ID	*Z*	*p*	Result
A	6.730	<.001	Bilateral
B	1.381	Non sig	No preference
C	−14.574	<.001	Unilateral
D	−11.72	<.001	Unilateral
E	−6.831	<.001	Unilateral
F	−2.375	<.005	Unilateral
G	−10.733	<.001	Unilateral
H	6.208	<.001	Bilateral
I	8.362	<.001	Bilateral
J	−3.23	<.001	Unilateral
K	−7.026	<.001	Unilateral
L	4.508	<.001	Bilateral

Note: Results of binomial tests. Subjects arranged in descending age order to be consistent with Table 1. Binomial test statistic *Z* and statistical significance *p* are presented for each subject.

proportion of time spent exploring materials or food ($p > .05$ in all cases). The only adult male in the group (subject A) was the only individual observed to scrounge fallen normal food (17 cases over 8 trials), whereas the highest-ranking female (subject D) was the only individual observed to steal normal food from others (13 cases over 8 trials). Scrounging and stealing food may have occurred in the baseline but were not recorded. Only the normal diet was scrounged, and only normal food was stolen except one case of stealing artichoke. The transportation of sweetcorn across the enclosure was performed by 9/12 lemurs; the three highest-ranking animals did not perform this behavior.

4 | DISCUSSION

Cognitive research in zoos is gaining both popularity and status (Garcia-Pelgrin et al., 2022; Hopper, 2017), but the paradigms employed in traditional cognitive laboratories do not translate to most zoos wishing to participate. Crucially, apparatuses in zoos need to accommodate social groups of animals and less controlled conditions than a laboratory setting. The current study evaluated the

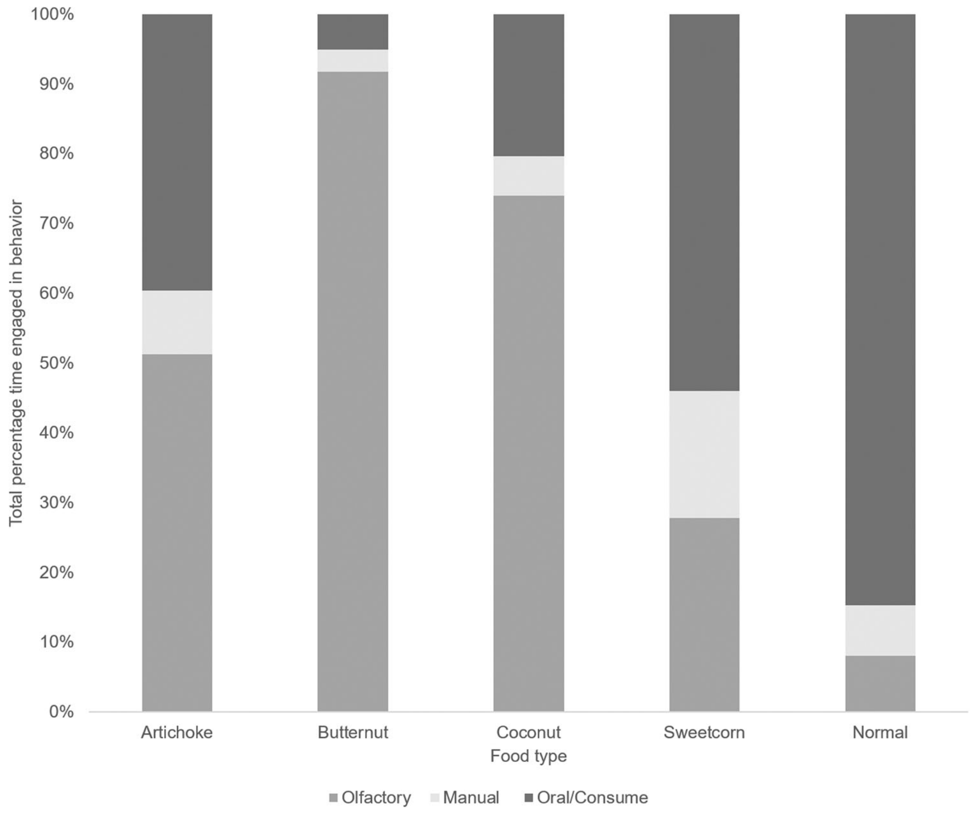

FIGURE 4 Behaviors used by lemurs to investigate and consume novel whole artichoke, butternut squash, coconut and sweetcorn in addition to the normal chopped diet. Troop medians are presented.

responses of a group of socially-housed lemurs towards a number of novel materials and whole foods, to inform the design of a new cognitive task apparatus suitable for typical zoo lemur groups. Preliminary studies of this kind are scarce in the literature but are important so that we avoid constructing apparatuses with design faults or restrictions which could be easily avoided.

4.1 | Exploration of materials

Exploration of surfaces and manipulanda was low (under 2 h of exploratory behavior was observed per lemur, across the study). When lemurs were within 0.5 m a material, they spent most of their time using it as a surface to rest and/or socialize (Figure 3), even when it was intended as a manipulandum. With hindsight, it would have been interesting to compare the use of surfaces and manipulanda in both horizontal and vertical positions. Surfaces were investigated around six times longer than manipulanda (8.9% time vs. 1.4% time) which suggests apparatus might be better placed horizontally, but surfaces also encouraged a lot more passive use (resting and socializing). These results suggest our new apparatus should be both vertical and narrow (without large ledges or platforms) to discourage passive use. The apparatus also needs to be low to the ground so that lemurs can bear weight on the ground, not the apparatus itself. Fortunately, lemurs had no obvious aversive responses to any of the materials presented, including the white plastic frame. If a zoo does not like an artificial aesthetic, plastic could be spray-painted brown or green to blend in. We found that stone was a highly preferred surface and therefore it could be used as a coating (i.e., a light concrete spray).

Lemurs preferred natural surfaces (wood, stone) over artificial surfaces (metal, plastic) if we take the relative duration of time in proximity as a proxy for preference. However, our results illustrate the importance of considering *how* exploration is performed and any consequences. Oral exploration of materials was low but when it did happen, wood was damaged by biting/chewing; this would affect the integrity of a future apparatus and also pose a risk to animal and researcher safety. We did not observe lemurs ingesting any wood (wild ring-tailed lemurs have been observed eating decaying wood, Simmen et al., 2006), but would still not use untreated wood in the future. We have previously encountered issues with wood used in enrichment warping or rotting when damp, and retaining scent (FEC, personal communication). We noticed during our posttrial clear-up that metal surfaces were hot to touch and also produced a lot of glare in the sun. This presumably explains why metal was the least preferred material (surface and manipulanda). Our study was undertaken during a northern hemisphere summer with a mean daily temperature min 52.7°F max 69.8°F (MET office, 2017). We do not recommend the use of metal in the future and recommend that if metal materials are used for apparatus, surfaces are regularly checked for temperature and glare (metal could also be prone to freezing if the environment is very cold).

Lemurs most commonly investigated materials by sniffing, followed by manual and oral exploration. This result is very useful for the development of future cognitive apparatuses because a species' sensory capabilities will affect their response (Plotnik et al., 2014; Shettleworth, 2010). Previous research on captive lemurs shows that both visual and olfactory cues are used to judge fruit ripeness, with a bias towards visual stimuli but this is dependent on the level of frugivory in each species (Rushmore et al., 2012). In the current study, lemurs scent-marked all materials, which poses a particular problem for untreated wood and stone because they are porous. Sophisticated scent communication in *Lemuridae* (see Scordato & Drea, 2007), means that they might find strong-smelling materials aversive or at least distracting, and could also mean that parts of the apparatus will be scent-marked to ward off conspecifics. Scent-marking is not a behavior that researchers could control during group testing, but attempts should be made to quantify scent-marking in the future. Using plastic materials in the future will assure scent marks, feces, and so forth can be cleaned away easily between trials.

Lemurs demonstrated low levels of manual dexterity during the study, using simple touching actions. We purposely attached the manipulanda loosely to the frame so that they could rotate, given that some "turning" actions have been incorporated into previous primate "artificial fruit" cognitive apparatus (e.g., Stoinski et al., 2001; Whiten et al., 1996). Turning actions were rare in our study, and previous research agrees lemurs have fewer complex manual actions than monkeys and great apes (Parker, 1974a, 1974b; Torigoe 1985). Because wild lemurs flexibly use different sized foraging patches (i.e., clumped, sparse) depending on resource availability (Ellwanger & Gould, 2011; Sauther, 1998; Soma, 2006) a horizontal "feeding patch" design is worth evaluating as an alternative or addition to a vertical apparatus. This could have features similar to experimental foraging patches for wild primates (Marshall et al., 2013) and the hole-board foraging apparatus used for farmed animals (Grimberg-Henrici et al., 2016; Roelofs et al., 2017). It would also be interesting to move away from the puzzle box designs already developed for lemurs, which consist of flipping, sliding, pushing or pulling one large lid with the snout or hand (Schnoell & Fichtel, 2012; Schnoell et al., 2014).

Our results show just over half (7/12) lemurs used one hand rather than two at a time to investigate materials. Bennett et al. (1995) found an even higher instance of unimanual handling in captive ring-tailed lemurs, but this was for small food items. In terms of future apparatus design, it seems logical to avoid anything which forces either unimanual or bimanual actions or forces a particular posture where a lemur must uncomfortably reach or balance. It is also important to randomize the arrangement of stimuli across space to avoid animals using pre-existing or developing new side biases (Tebbich et al., 2007).

4.2 | Exploration of whole foods

Similar to materials, foods received little time investment from lemurs (4.4% time exploring whole food vs. 3.5% time exploring normal diet). The very impenetrable outer shell of coconut led to low investigation, whereas we observed lemurs removing the leaves and husks from artichoke and sweetcorn. Lemurs showed low levels of food-handling dexterity due to the lack of a precision grip in prosimians (Holtkötter, 1997), and instead, they relied on using their teeth. These observations give us inspiration for the design of artificial fruit apparatuses for lemurs. Our results suggest kernels of sweetcorn might be a good option as a high-value food reward for future trials (but see Hopper et al., 2018 for a comprehensive approach).

A limitation of our study was that even though lemurs had time to freely choose between two resources provided each trial, "spending time with" is not necessarily the same as "liking/disliking" something (Dawkins, 1977). An animal may spend more time exploring one resource over another, without necessarily being strongly attracted to it, or deriving wellbeing benefits from it (Dawkins, 1977). However, because our tests were not a forced choice of resources (i.e., an animal did not have to make one choice or another), took place under normal social and housing conditions, and were associated with restful and social behaviors, we believe they are biologically valid. This being said, in the future we recommend taking more/less preferred areas of the enclosure into account and making sure this does not bias results.

4.3 | Social testing

We found two benefits of social testing that may translate to formal cognitive testing trials. First, normal social conditions promote more biologically valid results (Cronin et al., 2017; Torigoe, 1985). Our study troop was unaccustomed to experimental manipulation, so any manipulations of their social group may have adversely impacted their behavior. The second benefit was that female dominance did not affect exploration. However, even though we did not observe any effect of dominance on latency to contact or time spent exploring materials or food, we still think it is wise to design an apparatus that can be accessed by several individuals simultaneously, thus minimizing the potential for monopolization and aggression. The number of opportunities a lemur has to respond to an apparatus could be significantly restricted if they are displaced by other animals (Griffin & Guez, 2016; Rowe & Healy, 2014).

A potential limitation of social testing is that high- and low-ranking lemurs may steal or scrounge food respectively (O'Mara & Hickey, 2012; Schnoell & Fichtel, 2012). Lemurs in mixed-species enclosures will also steal food from heterospecifics (Dishman et al., 2009). Stealing and scrounging were observed in our study in response to the normal chopped diet. It is our opinion that stealing or scrounging are naturalistic cognitive strategies, and therefore should not be prevented by testing individuals alone or by stopping access to fallen/discarded food rewards. A study by Kulahci et al. (2018) experimentally reduced scrounging opportunities in socially-housed ring-tailed lemurs by creating a food puzzle that only released one food reward (a grape) at a time, but this

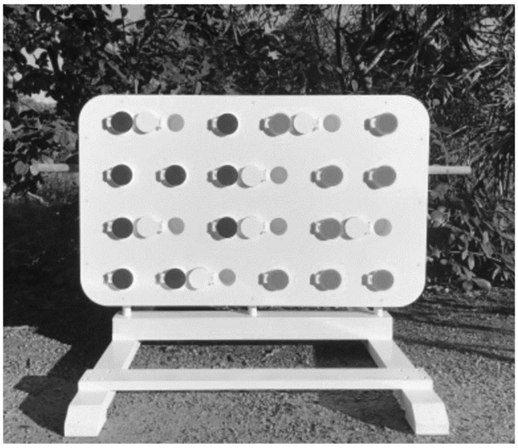

FIGURE 5 Lemur Bootcamp cognitive apparatus. Constructed from a white acrylic box (approx. 98 × 60 × 8 cm) slotted into a white wooden frame. The box has an arrangement of 24 equally-spaced circular chambers (5 cm diameter and 5 cm depth), each covered by a hinged door. The specific array shown above contains 12 (color 1) and 12 (color 2) randomly arranged doors, with one of these colors baited with a food reward (not shown).

protocol required the researcher to refill food multiple times in a session which could be argued to disturb the lemurs from their task.

Our study group was considered representative of "normal" zoo lemurs; they were housed in a walkthrough enclosure with a normal captive social grouping and dynamics. Therefore, we believe that our findings will be generalizable to other similar ring-tailed lemur groups. This being said, our dominance calculation on females will not be comparable to bachelor groups of lemurs, and in hindsight, we should have collected more social data on the troop as a whole to reflect their social hierarchy. There were large individual differences in the behavior of our study subjects (as illustrated by the large interquartile range values); other studies have revealed similar interindividual variation in lemurs (e.g., Santos et al., 2005; Stoinski et al., 2011). We assert that individual differences are both interesting and important for animal cognition studies (Boogert et al., 2018; Webster & Rutz, 2020). As the Lemur Bootcamp project progresses, we hope to quantify individual variation in cognitive responses, both within and between groups of lemurs. We also believe that studies similar to ours could be performed on putative enrichment materials, particularly when there will be a high monetary

TABLE 4 Design justifications for a new lemur cognitive testing apparatus.

Current study results	Design feature
Responses to materials	
Lemurs rested on horizontal surfaces.	The apparatus is built vertically with no large horizontal platforms or ledge to rest on. It is low to the ground, approximately the height of a bipedal *Lemur catta* (70 cm)
Lemurs chewed and damaged wood.	Manipulanda are not made from untreated wood.
Lemurs had no aversive responses to white plastic.	The front of the apparatus is made from sturdy, weather-proof, easy to clean plastic.
Metal got very hot and produced glare.	Surfaces and manipulanda are not made from mental.
Lemurs used simple touching with one or both hands.	Food is accessed via a simple action (i.e., opening a door) and no prior animal training is required. The food chamber doors are large and hinged. Once opened, doors are held by magnets
Responses to food	
Lemurs commonly sniffed materials.	The food chambers are constructed from plastic pipe to allow easy cleaning. The food scent across all chambers is controlled. All chambers contain food, but 'incorrect' chambers are covered by a layer of mesh so that food cannot be removed.
Social testing	
Lemurs used materials socially.	The apparatus is large enough to allow use by more than one lemur at a time. Cues are spread widely across the surface of the apparatus.
Lemurs climbed and jumped on materials.	The apparatus has a wide, heavy wooden base to prevent toppling over. The base is adjustable to accommodate uneven flooring.
Low-ranking lemurs scrounged food rewards from the floor.	The apparatus has a wide, clear space around it so that observers can clearly distinguish between retrieved and fallen/scrounged food.
Practicality	
Storage facilities at zoos are limited.	The apparatus has a compact design, with detachable wooden carry handles. The apparatus detaches from the base for transport. The front of the apparatus screws off to clean the food chambers.
The weather was variable.	The exterior of the apparatus is plastic, or a weatherproof wooden paint.

investment to build the final product, or if there are doubts over how certain manipulanda might function in a given zoo environment.

4.4 | Evidence-based cognitive apparatus design

The results of this study informed the design of a new cognitive apparatus with concealed food rewards within artificial "fruit" within an overall "tree" structure (Figure 5). The apparatus was designed to allow testing aspects of foraging cognition such as learning the association between food and particular cues or locations. The discussion above highlighted why several design choices were made, but these are consolidated in Table 4.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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