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Food-based enrichment and its influence on behaviour and display of stereotypies of three aye-ayes [*Daubentonia madagascariensis* (Gmelin, 1788)] at Frankfurt Zoo

Futtermotivierte Beschäftigung und ihr Einfluss auf das Verhalten und das Auftreten von Stereotypien bei drei Aye-Ayes [*Daubentonia madagascariensis* (Gmelin, 1788)] im Frankfurter Zoo

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Summary

The aye-aye (*Daubentonia madagascariensis*) is a nocturnal lemur with several physical particularities such as rodent-like teeth, enlarged ears, and elongated fingers that it uses for a specialised foraging strategy called "percussive foraging". Because many aye-ayes in human care display stereotypic behaviours, this study investigates whether food-motivated enrichment that encourages display of percussive foraging can alter the behaviour and elicit signs of improved welfare in three aye-ayes housed at Frankfurt Zoo, Germany.

We observed the aye-ayes in three husbandry conditions: control (standard housing), enriched, and unenriched. Data were collected by instantaneous (scan) sampling from may to august 2013. To evaluate success of the enrichment, we chose four behavioural indicators: display of stereotypic behaviours (SB), time spent out of sight, display of explorative behaviours, and behavioural variability (BV). We examined the influence of five factors (focal individual, enrichment condition, noise levels, visitors in front of the enclosures, and time of day) on the behavioural indicators to gain information about possible causal factors for behaviour changes.

Each behavioural indicator was influenced by the individual and at least one other factor. Display of SB was positively correlated with the number of visitors in front of the enclosures and noise. Aye-ayes showed more SB in the afternoons of the enriched condition than in the

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afternoons of the control condition. During noon (12.30-3.30 pm), time spent out of sight was positively correlated with noise levels and one aye-aye spent less time out of sight in the enriched compared to the unenriched condition. Two aye-ayes, both fully adult, displayed most explorative behaviours and highest BV in the enriched condition.

Our study presents examples of suitable food-based enrichment, and our results yield new valuable insights about factors that potentially influence SB in aye-ayes. However, because behavioural indicators were influenced by at least two factors, factors partly influenced each other, and the duration and sample size of the study were low, general conclusions about aye-aye behaviour cannot me drawn. Future studies should investigate the influence of noise and visitors on aye-ayes in more depth and aim to develop and evaluate effective strategies or enrichments to reduce stereotypies. As we did not observe indications that food-based enrichment compromised welfare and BV increased in two focal individuals in the enriched condition, we advocate for the use of foraging enrichment for aye-ayes until more data is available.

Keywords: aye-aye, stereotypy, ARB, enrichment, zoo

Introduction

Scientifically managed zoos and aquaria continuously work on refining husbandry best practices (Mellor et al., 2015; Swaisgood & Shepherdson, 2005). Nevertheless, a considerable number of individuals in zoological collections display stereotypies or other abnormal repetitive behaviours (ARBs) (Mason et al., 2007; Mason & Latham, 2004; Shyne, 2006).

Stereotypies are invariant, repetitive behaviours without an obvious goal or function (Dantzer, 1991; Broom, 1983; Mason, 1991a, b) that are often a sign of impaired welfare, especially while animals develop them (Dantzer, 1991; Mason, 1991a; Mason & Latham, 2004). However, as stereotypies can change over time (Tatemoto et al., 2022) and emancipate (i.e., become disassociated) from their original stimulus, they may in some cases indicate 'scars' of previous impaired welfare (Mason, 1991a, b). As the relation between stereotypies and current welfare is not yet completely understood (Mason, 1991a; Swaisgood & Shepherdson, 2005), the presence of stereotypic behaviours alone is not sufficient to evaluate animal welfare (Broom, 1983; Broom, 1991; Mason & Mendi, 1993).

Stereotypies can be influenced by various factors such as enclosure features (Bashaw et al., 2001; Mallapur & Chellam, 2002), age (Gruber et al., 2000; Mason, 1993; Mason & Vickery, 2004), or time of day (Carlstead, 1998; Mason, 1993; Mason & Vickery, 2004). Noise levels in zoos, for example, are considerably higher than in the wild (Morgan & Tromborg, 2007), and elevated noise has been shown to affect behaviour and cause signs of stress in several species (Clark & Melfi, 2012; Morgan & Tromborg, 2007; Swaisgood & Shepherdson, 2006). Certain environmental factors, e.g. zoo visitors, can influence animals in several ways that potentially increase stress and might compromise welfare. Zoo visitors spread odours, increase noise levels, behave in an unpredictable manner, and can sometimes enter the flight distance (Morgan & Tromborg, 2007). Visitor presence has been shown to increase aggression (Chamove et al., 1988; Glatston et al., 1984), reduce species-typical behaviours (Glatston et al., 1984; Wood, 1998), and increase levels of stereotypy and other ARBs (Chamove et al., 1988; Mallapur et al., 2005) in different primate species.

Taxa differ in their most common types of ARBs as well as prevalence of stereotypies (Novak & Bollen, 2006; Rushen & Mason, 2006; Swaisgood & Shepherdson, 2006). Levels of stereotypies in prosimians are with 7-13% comparatively low compared to levels in other primates (Novak & Bollen, 2006; Tarou et al., 2005). However, many adult zoo-housed aye-ayes [*Daubentonia madagascariensis* (Gmelin, 1788)] display stereotypic behaviours (Rachel Cowen, Aye-aye EEP Coordinator, Durrell Wildlife Conservation Trust, pers. comm.). Often, whole-body stereotypies are displayed (pers. obs.), as reported for other lemurs (Tarou et al., 2005). Until now, the reasons why stereotypies seem to be so frequent in aye-ayes are not understood.

The most common method to tackle stereotypies is environmental enrichment (Mason et al., 2007; Swaisgood & Shepherdson, 2005; Swaisgood & Shepherdson, 2006). The applied environmental change (i.e., enrichment) must lead to an improvement of the animal's situation, i.e., meet their needs, to be effective (e.g., Tatemoto et al., 2022). Therefore, enrichment is often designed to cater to special adaptations of the focal species, e.g., gnawing bricks and tunnels for voles (Kapusta et al., 2022) versus puzzle feeders for primates (de Rosa et al., 2003; Gilloux et al., 1992). Aye-ayes are highly specialized in their foraging behaviour, called percussive foraging (Erickson, 1994). They use the claw of their elongated third finger to tap on wood and use their hearing to detect insect larvae. Then, they open the wood with their rodent-like teeth and extract the prey with their third or fourth finger (Fig. 1). Hence, food-motivated enrichment seems to be a good starting point for enriching aye-ayes with the goal of reducing stereotypic behaviours and giving them opportunities to perform preferred behaviours.

Fig. 1: Anatomical specialisations of the aye-aye. A & B: hand with elongated third and fourth finger, C: foot, D: rodent-like incisivi used for gnawing. Photos: Miriam Göbel

Therefore, we investigated whether food-motivated enrichment can alter the behaviour and thereby elicit signs of improved welfare displayed by three aye-ayes housed at Frankfurt Zoo, Germany. To do so, we observed the aye-ayes in an enriched and an unenriched condition, as well as control intervals. Furthermore, we examined whether noise levels, visitors in front of the enclosures, and time of day influence their behaviour to gain information about possible causal factors for stereotypies in aye-ayes.

To evaluate the success of the enrichment, we chose four behavioural indicators:

1) **Reduction of display of stereotypic behaviours (SB).** As described above, the display of stereotypic behaviours may be associated with impaired welfare. Reducing or eliminating stereotypy by providing enrichment is considered a sign of improved welfare, as enrichment can reduce stereotypy by reducing underlying frustrations and stressors, or by providing opportunities to engage in preferred behaviours (Mason et al., 2007).

2) **Reduction of time spent out of sight.** The aye-ayes at Frankfurt Zoo are housed in a combination of display enclosures with large glass windows for visitors to see through and smaller non-visible enclosures ('boxes'). The display enclosures are much larger, well furnished, and food is usually provided there. The boxes are comparatively small and therefore barely furnished. Nevertheless, the aye-ayes spent considerable amounts of time in the boxes during previous observations (Wolter, 2010; Zizka, 2013). Because we assume that the aye-ayes use the boxes mainly to retreat from stressors elicited by visitors, daily routine works in the enclosures, and co-housed individuals, we regard a reduction of the amount of time spent out of sight to be a sign of improved welfare.

3) **Increase of explorative behaviours,** (locomotion, exploration, enrichment interaction). In previous studies (Wolter, 2010; Zizka, 2013) the aye-ayes displayed low amounts of explorative behaviours in comparison to wild aye-ayes (Ancrenaz et al., 1994). As a natural behavioural budget is often used as an indicator for positive welfare in human care (Young, 2003; Morgan et al., 1998), and explorative behaviours have been associated with positive welfare (Poole, 1998; Mench, 1998), we regard the increase of explorative behaviours as a sign of successful enrichment.

4) **Increased behavioural variability (BV),** i.e., number of different behaviours displayed during one observation unit. As zoo animals often show low behavioural diversity in comparison to their wild conspecifics, increased behavioural diversity can be a sign of improved welfare (Clark & Melfi, 2012; Shepherdson et al., 1993; Young, 2003). The food-motivated enrichment we provide is supposed to give the aye-ayes more opportunities to display general foraging behaviour as well as percussive foraging. Moreover, it allows the aye-ayes to choose to interact with an enrichment device that would otherwise not be in the enclosure. Therefore, we regard increased behavioural variability as an indicator of successful enrichment.

We predict that the aye-ayes show a reduction of SB and time spent out of sight as well as an increase of explorative behaviours and BV in the enriched condition. We expect the opposite trend in the unenriched condition as well as for high noise levels and high visitor numbers in front of the enclosures.

Methods

Between 20 May 2013 and 16 August 2013, MG observed two male and one female aye-aye housed at Frankfurt Zoo (Tab. 1). The aye-ayes were housed in two enclosure complexes, all operated in an artificial night, so that the animals were active during working and visitor hours. The males were housed with grey mouse lemurs (*Microcebus murinus*).

The aye-ayes were exposed to three different enrichment conditions: enriched, unenriched, control (Tab. 1). The control condition equated to the standard husbandry at Frankfurt Zoo that the aye-ayes were used to and which included regular provision of some enrichment. In the enriched condition, the aye-ayes received considerably more food-based enrichment than during their normal husbandry/control (Tab. 2). In the unenriched condition, the aye-ayes received only a very simple form of food-based enrichment, an open bamboo stick to deliver the daily portion of wax moth larvae (*Galleria mellonella*), so that all food was easily accessible. We did not change the diet or amount of food between conditions to prevent an influence on behaviour. Instead, the food used to equip the enrichment was taken off the normal diet.

Tab. 1: Information on focal animals. Information relevant for both males highlighted in grey print.

Focal Animal	Kintana	Malala	Kimala
Sex	female	male	male
Birth date	11/02/2005	08/08/1999	10/01/2011
Birthplace	Bristol Zoo, UK	Jersey Zoo, UK	Frankfurt Zoo, Germany
Age at observations	8 (adult)	13-14 (adult)	2 (adolescent)
Comments	hand-raised		son of Kintana & Malala
Enclosures	K14 (63.3 m^3) + B3 (1 m^3) = 64.3 m^3	K 13 (62.5 m^3) + B1 (7 m^3) = 69.5 m^3	
Length of glass panel	5.5 m	5.4 m	
Co-housed species	-	grey mouse lemur (*Microcebus murinus*)	

Tab. 2: Food-based enrichment provided to the aye-ayes. C = control condition, EN = enriched condition, UN = unenriched condition.

Name	Condition	Enrichment	Behavioural goals for enrichment interaction
Open bamboo stick	UN	A bamboo stick is cut and filled with wax moth larvae. The openings are closed with moist paper.	Easy access to food for the aye-ayes
Rugel	C & EN	Wooden block with several holes (approx. 3 cm deep). The holes are filled with wax moth larvae and closed with moist paper. The aye-ayes must find the larvae and extract them.	Percussive foraging
Filled bamboo stick (Figure 2)	C & EN	A small hole (approx. 0.5 cm) is drilled in a bamboo stick. The stick is filled with yoghurt or wax moth larvae. The aye-ayes must extract the food with their specialised fingers or gnaw the bamboo stick open.	Percussive foraging, gnawing
Large bamboo with holes (Figure 2)	EN	Several holes of 3 – 8 mm are drilled into a large and dry (hard), bamboo. The bamboo is filled with wax moth larvae. As the larvae can move within the bamboo, their extraction is more complicated and time-consuming	Percussive foraging (increased difficulty compared to filled bamboo stick or rugel)
Wood block with hole (Figure 2)	EN	In the middle of the diameter of a piece of soft wood (5-15 cm diameter, 15-20 cm length), a hole of approx. 12 cm is drilled. Wax moth larvae are given into the hole which is then closed firmly with a wooden dowel of approx. 4 cm length.	Percussive foraging, gnawing
Wood box (Figure 2)	EN	A hollow wood box is filled with paper and wax moth larvae or mealworms (*Tenebrio molitor*). It is then closed firmly.	Percussive foraging, gnawing, opening the box with other behaviours
Distributed larvae of *T. molitor*	EN	Mealworms are scattered in the enclosure, mainly in open coconut shells that are hanging at several point in the enclosure, to prevent ingestion of substrate and parasite transmission.	Increase of exploration
Filled pasta / pinecones	EN	Approx. 7 pasta per animal are filled with soft foods or three pinecones are filled with dried fruit or peanuts and then hidden in the enclosure.	Increase of exploration

Fig. 2: Enrichment devices. Top left: woodblock with hole, top right: large bamboo with holes, below left: filled bamboo stick, below right: wood box. Photos: Miriam Göbel

Data collection

We observed the aye-ayes from 9.30 am to 6.30 pm (full artificial night) and used a pseudo-randomised observation schedule that covered all observation times and focal animals equally. In total, every aye-aye was observed for six full nights in the control condition and three full nights in the enriched and unenriched condition, respectively (Fig. 3).

	19.05.-08.06.	09.06.-29.06.	30.06.-13.07.	14.07.-04.08.	05.08.-16.08.
Males	Control	Enriched	Control	Unenriched	Control
Female	Control	Unenriched	Control	Enriched	Control

Fig. 3: Study setup. Observations conducted in 2013.

We used instantaneous sampling for the single-housed female and instantaneous scan sampling for the co-housed males (Altmann, 1974). Observation units had a duration of 30 min with a sample interval of 15 s. At every sample point, we recorded behaviour as defined in the ethogram (Table 3), number of visitors in front of the enclosure, and noise level. The ethogram was adapted from previous studies (Wolter, 2010, Zizka, 2013) on the aye-ayes at Frankfurt Zoo and extended if necessary. We noted visitors in max. 1.5 m distance to the enclosure. For one to five visitors, we noted the exact number, six to nine visitors were noted as 7.5, ten or more visitors were noted as ten. We measured noise levels with a sound level meter (Voltcraft SL-100). Settings were 'lower measurement range' (30-100 dB), 'characteristic C', and 'fast' changes of sound levels. Accuracy is ± 2 dB at one kHz. We noted data in an excel sheet (Microsoft Office Excel 2007) and recorded special events ad libitum.

Tab. 3: Ethogram. Adapted from Wolter (2010) and Zizka (2013) and translated to English.

Behaviour	Description
Locomotion	Movement like walking, running, climbing, or jumping, and "slow locomotion" (Ancrenaz at al., 1994), if the animal does not explicitly show one of the other listed behaviours, especially exploration, at the sampling point.
Exploration	Sniffing, looking at, gnawing, and touching of objects other than food and enrichments. "Percussive foraging" (Erickson, 1994). Brief stopping of movements, brief sitting, and erecting on hind limbs, as the aye-ayes use to listen and sniff their environment (with visible movements of nose and ears).
Feeding	Feeding, transport and exploration of food items, defecating, urinating.
Resting	Lying on branches and sitting in positions in which the tail is curled around the body. All positions in which the head is rested on an object.
Comfort	Cleaning, scratching, stretching, yawning, and hanging on hind limbs.
Stereotypy	Display of individually defined stereotypical habits or established stereotypies. *Stereotypical habits* were defined as movement patterns that were displayed at least three times consecutively (without interruption) at the same position in the same observation unit. They were noted only, if this definition had been met for the respective observation unit. *Established stereotypies* were described by Wolter (2010) or Zizka (2013) for the respective individual with the same behaviour pattern and location in the enclosure. They were noted from first occurrence. Stereotypical habits were re-defined as established stereotypies if the definition for stereotypic habit was met three times at the same location with the same behaviour pattern within one observation unit.
Enrichment interaction	Exploring, touching, or transport of enrichments. Eating from enrichments (as exploring and feeding could often not be clearly distinguished).
Out of sight	Stay in box enclosures, short stay in sleeping box, or if displayed behaviours could not be clearly identified.
Territorial behaviour	Nest building, transport of nesting material, marking with anal glands.
Interaction	Vocalisations, sniffing of active touching of other individuals (play, fight), following another individual in a distance less than a body length. Inactive touching (e.g., during feeding while sitting next to each other) was not recorded as interaction.
Mating	Mating between a male and a female. Mating attempts between males were not recorded as mating but as interaction.
Sleeping	More than 15 min spent in nest.

Data analysis

We noted behaviours during observations and calculated sum of behaviour as well as means of visitors in front of the enclosure and noise level measurements [dB] per observation unit with Microsoft Office Excel 2007. To measure the indicators display of SB and time spent out of sight, we used the count of the respective behaviour as defined in the ethogram. To calculate the indicator explorative behaviours, we added the counts for the behaviours locomotion, exploration, and enrichment interaction, as this definition better reflects explorative behaviour of aye-ayes in the wild as described by Ancrenaz et al., (1994). We computed BV by counting the number of different behaviours that were displayed during one observation unit. Because wax moth larvae were delivered in a bamboo stick during the unenriched condition and holding the stick or feeding from it were defined as enrichment interaction, the potential number of behaviours was the same throughout conditions.

Statistical analyses were performed in R version 3.0.0 (R Core Team), using the packages *car* (Fox & Weisberg, 2011), *sciplot* (Morales, 2011), and *multcomp* (Hothorn et al., 2008). We computed Poisson generalised linear models (GLMs) and multifactorial analysis of variance (ANOVA) to test how the factors individual (Malala, Kimala, Kintana), enrichment condition (enriched, unenriched, control), time of day (morning 9.30 am-12.30 pm, noon 12.30-3.30 pm, afternoon 3.30-6.30 pm), mean noise level, and mean number of visitors in front of the enclosure, influence the defined behavioural indicators. We visually checked data for normal distribution, transformed data, if necessary (SB, explorative behaviours, out of sight: asin(sqrt()); BV: not transformed), and inspected residuals for over-dispersion using the *car* package (Fox & Weisberg, 2011). Due to our limited sample size, we only considered effects on behaviour that were caused by maximally two factors. For significant effects (significance level α=0.05) we performed Tukey-Test for the categorical predictors (individual, enrichment condition, time of day) and Spearman's rank correlation coefficient for the continuous predictors (noise level, number of visitors) as post hoc tests. We used Bonferroni correction to adjust significance levels if several post-hoc tests were performed on the same data set.

Results

The three aye-ayes differed substantially in their behaviour (Tab. 4). The female, for example, spent over 50% of observation time sleeping, whereas the males slept less than 3%. Noise levels and number of visitors in front of the enclosures were strongly positively correlated (Spearman's rank correlation: $p<0.001$; $r_S=0.72$; n=648) but the not stable throughout observations; there were less visitors present in the enriched than in the control condition and visitor numbers were highest at noon, intermediate in the morning and lowest in the afternoon. Noise levels were lower in the afternoon than at the other times of day and higher in the control condition than in the enriched and unenriched condition (Tab. 5). We performed ANOVAs (Tab. 6) to identify factors that influence behavioural indicators and conducted post-hoc tests for significant results.

Tab. 4: Proportion of behaviours displayed by the focal individuals in the different conditions. C = control condition, EN = enriched condition, UN = unenriched condition. Malala = adult male, Kimala = subadult male, Kintana = female.

Focal Animal	Malala			Kimala			Kintana		
Condition	C	EN	UN	C	EN	UN	C	EN	UN
Locomotion	15.5	17.4	16.8	22.2	23.7	20.7	3.3	7.6	4.7
Exploration	17.7	15.2	17.2	31.3	26.4	30.4	6.0	10.8	8.0
Feeding	12.3	14.2	10.8	11.9	11.3	9.6	3.1	3.9	5.4
Resting	0.5	0.5	0.9	0.6	0.5	0.2	0.3	0.0	0.1
Comfort	6.1	4.0	7.6	5.5	3.9	5.4	7.5	7.2	7.2
Stereotypy	18.7	17.6	18.6	3.1	5.0	6.3	3.0	9.0	8.6
Enrichment interaction	1.5	7.9	1.1	3.9	9.8	2.1	0.9	6.9	0.0
Out of sight	24.8	20.9	24.2	17.1	15.6	19.9	7.0	5.8	11.7
Territorial behaviour	0.1	0.1	0.2	0.6	0.1	0.9	0.3	0.3	0.6
Interaction	2.3	2.2	2.7	2.6	2.2	3.1	0.0	0.0	0.0
Mating	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sleeping	0.7	0.0	0.0	1.3	1.3	1.3	68.6	48.5	53.8

Tab. 5: Noise levels and number of visitors in front of the enclosures in dependence on time of day and enrichment condition. Test: Tukey contrasts. Significance level after Bonferroni correction: $\alpha_{corrected}$ =0.008 (α=0.05/6 [number of tests per data set]). Significant results are highlighted in bold print.

Time of day	Noise level (n=648)		Condition	Noise level (n=648)	
Morning/Noon	p=0.027	z= 2.584	Enriched/Control	**p<0.001**	**z= 4.121**
Morning/Afternoon	**p=0.001**	**z= -6.238**	Enriched/Unenriched	p = 0.92	z= -0.398
Noon/Afternoon	**p=0.001**	**z= -8.819**	Control/Unenriched	**p < 0.001**	**z= -4.581**
Time of day	Visitors (n=648)		Condition	Visitors (n=648)	
Morning/Noon	**p<0.001**	**z = 5.522**	Enriched/Control	**p<0.001**	**z= 3.713**
Morning/Afternoon	**p<0.001**	**z = -5.172**	Enriched/Unenriched	p = 0.27	z= 1.534
Noon/Afternoon	**p<0.001**	**z = -10.694**	Control/Unenriched	p = 0.13	z= -1.942

Tab. 6: Results of the executed ANOVAs. n = number of observation units. The response variable is the counted display of indicated behaviour during one observation unit. Grey print: results not conclusive due to interaction terms of several factors for the respective behavioural indicator; n.s.: not significant; x: not tested due to interaction terms of more than two factors for the respective factors and behavioural indicator. Interactions terms that were never significant are not displayed.

	Stereotypic behaviours n = 648	Explorative behaviours n = 648	Out of sight n = 648	Behaviour variability n = 648
Individual	F = 265.201 df = 2 p <0.0001	F = 230.812 df = 2 p < 0.0001	F = 39.783 df = 2 p < 0.0001	F = 551.12 df = 2 p < 0.0001
Condition	F= 12.514 df = 2 p = 0.0019	F = 25.570 df = 2 p < 0.0001	F = 14.716 df = 2 p < 0.00064	F = 32.18 df = 2 p < 0.0001
Noise level	F = 4.675 df = 1 p = 0.031	n.s.	F = 3.887 df = 1 p = 0.049	n.s.
Visitors	F = 12.709 df = 1 p < 0.00036	n.s.	n.s (p = 0.051)	n.s.
Time of day	F = 205.717 df = 2 p < 0.0001	n.s.	n.s.	F = 25.60 df = 2 p < 0.0001
Individual: Condition	n.s.	F = 12.678 df = 4 p = 0.013	F = 10.406 df = 4 p = 0.034	F = 11.17 df = 4 p = 0.025
Noise level: Visitors	n.s.	F = 5.596 df = 1 p = 0.018	n.s.	n.s.
Individual: Time of day	F = 44.041 df = 4 p < 0.0001	x	n.s.	F = 248.97 df = 4 p < 0.0001
Condition: Time of day	F = 11.099 df = 4 p = 0.026	x	n.s.	F = 12.10 df = 4 p = 0.017
Noise level: Time of day	n.s.	x	F = 11.340 df = 2 p = 0.0035	n.s.

Stereotypic behaviours

Display of SB was positively correlated with number of visitors in front of the enclosures (Spearman's rank correlation: $p < 0.001$; $r_s = 0.20$; $n = 648$) and noise level (Spearman's rank correlation: $p < 0.001$; $r_s = 0.18$; $n = 648$). While total levels of stereotypy (Tab. 4) were not influenced by the enrichment condition, the aye-ayes showed more SB in the afternoons of the enriched condition than in the afternoons of the control condition (Tukey contrasts, $p = 0.013$, $z = -2.831$, $\alpha_{corrected} = 0.016$). Furthermore, we found a significant interaction term between individual and time of day (Tab. 6). Overall, the percentage of SB displayed tended to decrease in the course of the day in all aye-ayes, but not all differences between all times of day were significant for all individuals (Tab. 7, Fig. 4).

Tab. 7: Display of stereotypic behaviours in dependence of individual and time of day. Test: Tukey Contrasts. Significance level after Bonferroni correction: $\alpha_{corrected}$ =0.016 (α=0.05/3[number of tests per individual]). Malala = adult male, Kimala = subadult male, Kintana = female. Significant results are highlighted in bold print.

	Malala (n = 216)		Kimala (n = 216)		Kintana (n = 216)	
Morning/Noon	**p < 0.001**	**z = -4.204**	p = 0.17	z = -1.815	**p < 0.001**	**z = -5.404**
Morning/Afternoon	**p < 0.001**	**z = -12.757**	**p < 0.001**	**z = -5.503**	**p < 0.001**	**z = -6.100**
Noon/Afternoon	**p < 0.001**	**z = -8.552**	**p < 0.001**	**z = -3.688**	p = 0.12	z = -2.151

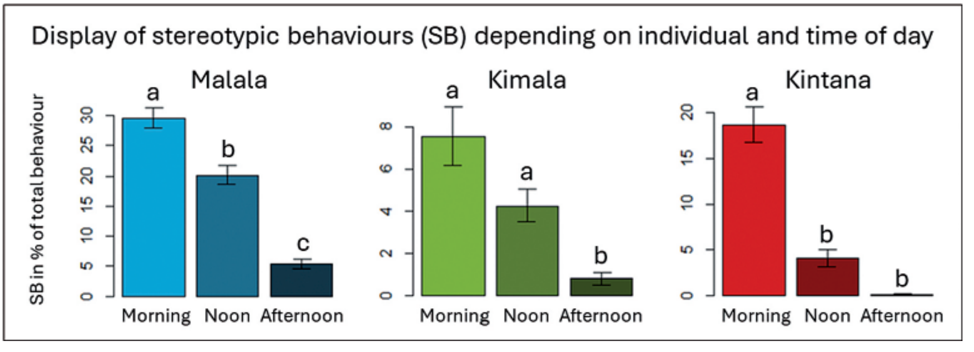

Fig. 4: Display of stereotypic behaviours (SB) in percent of total behaviour per individual and in dependence of time of day. Malala = adult male, Kimala = subadult male, Kintana = female.

Time spent out of sight

For the time the aye-ayes spent out of sight we found a significant interaction term between individual and enrichment condition (Tab. 6). Although the time spent out of sight did not vary between enrichment conditions in the males, the female spent less time out of sight in the enriched compared to the unenriched condition (Tukey contrasts, $p = 0.0096$, $z = 2.929$, $\alpha_{corrected} = 0.016$). Time out of sight was influenced by another interaction term of noise levels and time of day. During noon, time spent out of sight was positively correlated with noise levels (Spearman's rank correlation: $p = 0.0018$, $r_s = 0.24$; $n = 216$, $\alpha_{corrected} = 0.016$).

Explorative behaviours

Explorative behaviours were influenced by an interaction term between noise levels and number of visitors (as suggested by the correlation between visitors and noise levels) as well as an interaction term of individual and enrichment condition (Tab. 8, Fig. 5). The adult male displayed more explorative behaviours in the enriched (40.5%) compared to the control condition (34.7%) whereas the female displayed more explorative behaviours in the enriched (25.3%) compared to the control (12.7%) and unenriched condition (23%). Enrichment condition did not influence explorative behaviours of the subadult male.

Tab. 8: Display of explorative behaviours in dependence of individual and enrichment condition. Test: Tukey Contrasts. Significance level after Bonferroni correction: $\alpha_{corrected}$ =0.016 (α=0.016/3[number of tests per individual]). Malala = adult male, Kimala = subadult male, Kintana = female. Significant results are highlighted in bold print.

	Malala (n = 216)		Kimala (n = 216)		Kintana (n = 216)	
Enriched/Control	**p = 0.016**	**z = -2.763**	p = 0.58	z = -0.992	**p = 0.005**	**z = -3.146**
Enriched/Unenriched	p = 0.14	z = -1.881	p = 0.10	z = -2.036	**p < 0.001**	**z = -4.369**
Control/Unenriched	p = 0.83	z = 0.587	p = 0.36	z = -1.359	p = 0.30	z = -1.484

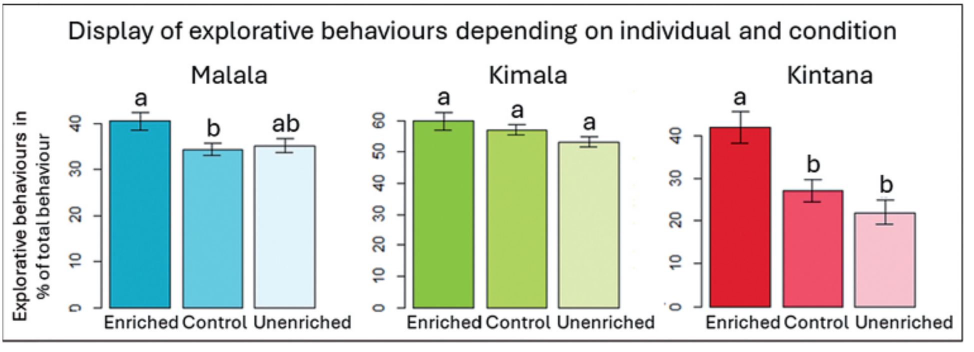

Fig. 5: Display of explorative behaviours in percent of total behaviour per individual in dependence on enrichment condition. Malala = adult male, Kimala = subadult male, Kintana = female.

Tab. 9: Behavioural variability, i.e., number of different behaviours displayed during one observation unit, in dependence on individual, enrichment condition, and time of day. Test: Tukey contrasts. Significance level after Bonferroni correction: $\alpha_{corrected}$=0.008 (α=0.05/6 [number of tests per data set]). Malala = adult male, Kimala = subadult male, Kintana = female. Significant results are highlighted in bold print.

	Malala (n = 216)		Kimala (n = 216)		Kimala (n = 216)	
Enriched/Control	**p = 0.005**	**z = -3.130**	p = 0.18	z = -1.780	**p = 0.002**	**z = -3.367**
Enriched/Unenriched	p = 0.098	z = -2.057	p = 0.67	z = -0.857	p = 0.25	z = -1.591
Control/Unenriched	p = 0.73	z = -0.756	p = 0.71	z = -0.791	p = 0.28	z = 1.531
Morning/Noon	p = 0.028	z = 2.568	p = 0.21	z = 1.687	**p < 0.001**	**z = -6.539**
Morning/Afternoon	**p < 0.001**	**z = 5.992**	**p < 0.001**	**z = 4.217**	**p < 0.001**	**z = -10.621**
Noon/Afternoon	**p = 0.002**	**z = 3.424**	p = 0.031	z = 2.530	**p < 0.001**	**z = -4.082**
	Morning (n = 216)		Noon (n = 216)		Afternoon (n = 216)	
Enriched/Control	**p = 0.001**	**z = -3.486**	p = 0.017	z = -2.742	p = 0.76	z = -0.707
Enriched/Unenriched	p = 0.53	z = -1.073	p = 0.63	z = -0.910	p = 0.50	z = -1.218
Control/Unenriched	p = 0.063	z = 2.246	p = 0.21	z = 1.691	p = 0.82	z = -0.596

Behavioural variability

Behavioural variability was influenced by three interaction terms: animal and enrichment condition, animal and time of day, and enrichment condition and time of day (Tab. 6). The adult aye-ayes showed a higher BV in the enriched compared to the control condition but intermediate BV in the unenriched condition, whereas BV of the subadult male was not influenced by enrichment condition (Tab. 9, Fig. 6). Behavioural variability of the adult male was highest in the evening, in the subadult male it was higher in the evening compared to the morning. The female, however, showed decreasing BV in course of the day (Tab. 9, Fig. 6). Only in the mornings, BV was higher in the enriched compared to the control condition (Tab. 9).

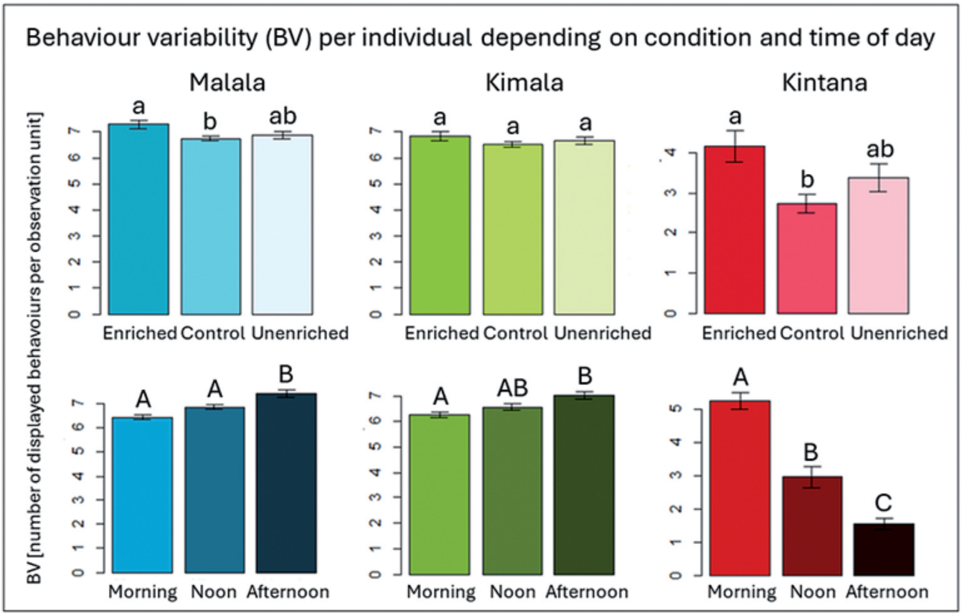

Fig. 6: Behaviour variability, i.e., number of behaviours displayed during one observation unit, per individual in dependence on enrichment condition and time of day. Malala = adult male, Kimala = subadult male, Kintana = female.

Discussion

In this study, we observed three aye-ayes in three enrichment conditions. The focal animals are partly related and housed in the same enclosures in the same zoo. Therefore, and even more importantly because of the small sample size, no general conclusions about ARBs in aye-ayes can be drawn from this study. Nevertheless, as to our knowledge no peer-reviewed studies on enrichment and stereotypic behaviours on aye-ayes have been published, our work provides valuable first insights.

We found that the focal individuals differed in the display of every pre-defined behavioural indicator for successful enrichment. As the aye-ayes have different sexes and ages, this is not surprising. Yet, looking into which behavioural indicator was influenced by which factors might yield information about successful enrichment for aye-ayes.

Stereotypic behaviours were influenced by all investigated factors. Number of visitors in front of the enclosures and noise levels were both weakly positively correlated with display of SB. It is possible that visitors may spend more time in front of the enclosures if aye-ayes display SB. However, Wolter (2010) found a strong positive correlation between total number of zoo visitors per month and average display of SB (Spearman's rank correlation: r=0.92 for the adult male, r=0.74 for the female), suggesting that higher visitor numbers encourage display of SB in the focal animals. An increase of abnormal behaviours related to visitors has been shown for other primate species, as lion-tailed macaques (*Macaca silenus*; Mallapur et al., 2005) and mandrills (*Mandrillus sphinx*; Chamove et al., 1988). Yet it remains unclear what causes the effects visitors have, i.e., whether visual, acoustic, and/or olfactory stimuli are decisive. Future studies should investigate how zoo visitors affect the behaviour of aye-ayes and how exposure to the stimuli that affect the aye-ayes can be reduced.

Time of day also influenced display of SB. Although the effect was not always significant, average display of SB decreased in the course of the day in all focal individuals (Tab. 7, Fig. 4). At the same time, the noise level was lowest in the afternoon and the number of visitors was highest in the morning and lowest in the afternoon. Because of the correlations between visitor numbers and noise levels with SB, the average decrease of SB over the day might be elicited by long-term effects of visitors and noise. In other species, display of stereotypic behaviour has been related to time of day (e.g., in Asian black bear (*Ursus thibetanus*) and sun bear (*Helarctos malayanus*; Mason & Vickery, 2004)), as well as feeding times (Clubb & Vickery, 2006; Mason & Vickery, 2004). Interestingly, even though the enrichment condition did not affect total display of SB in this study, the aye-ayes showed more SB in the afternoons of the enriched condition than in the afternoons of the control condition. This was the time when aye-ayes received most food. As enrichment can increase arousal, there might be similarities to "pre-feeding excitement" that has been described for carnivores (Mason, 1991a). Future studies should investigate in more detail why SB in these aye-ayes seem to depend on time of day and what measures can be taken to improve the environment of the aye-ayes at times when display of SB is high.

Even though the aye-ayes usually interacted with all provided enrichment, which led to an increase in enrichment interactions of more than 5% for all individuals in the enriched condition (Tab. 4), the overall level of SB could not be reduced by the enrichment. Stereotypic behaviours can emancipate from their initial causes and become habit-like and more resistant to change over time (Mason, 1991a, b). Nevertheless, several studies show that enrichment can reduce display of repetitive behaviours in many species (Shyne, 2006, Swaisgood & Shepherdson, 2005). Maybe, the amount of food that was freely available was still too high or the time that the aye-ayes had to spend with the enrichment to obtain the food inside was not high enough for the enrichment to be effective. An alternative explanation is that the utilised enrichment did not tackle the causes of the SB or that the duration of the enriched condition was too short to influence amount of SB displayed. Therefore, it should be assessed whether increased provision of food-motivated enrichment is effective if given on a long-term basis or whether there are other enrichment options that are more effective for aye-ayes.

During noon, the aye-ayes spent more **time out of sight** if noise levels were higher. As generally noise levels were highest at noon, this suggests that aye-ayes might prefer to retreat to more remote areas (the boxes) if it gets too loud. Effects of noise levels on behaviour have been found for several species: giant pandas (*Ailuropoda melanoleuca*) change their behaviour and activity budget depending on noise (Owen et al., 2004; Powell et al., 2006). About half of the individuals of twelve mammalian species including five primate species increased their vigilance behaviour with increasing sound levels (Quadros et al., 2014). And in a case study, pied tamarins (*Saguinus bicolor*) frequented an off-exhibit area more often if it was quieter than the on-exhibit area but not when noise levels were the same (Wark et al., 2023). Although all cited studies were conducted with low numbers of individuals per species, it seems reasonable to conclude that aye-ayes might react to high noise levels by retreating to quite areas. Follow-up studies should investigate the effects of noise levels on aye-ayes and their welfare.

Further, the female spent less time out of sight in the enriched than in the unenriched condition. If the time she spent out of sight and with enrichment interaction is combined, she spent roughly the same amount with the two behaviours in the enriched (12.7%) and the unenriched (11.7%) condition (Tab. 4). This is not true for the control condition (7.9%). However, she spent much more time sleeping in the control (68.6%) than in the enriched (48.5%) and unenriched condition (53.8%), so it seems like she prefers interacting with the enrichment over spending time out of sight. Several studies have already suggested the use of enrichment to increase visibility of zoo animals (Foerder et al., 2020, Puehringer-Sturmayr et al., 2023, Turnock & Moss, 2015). Our study reinforces that this approach might be suitable for aye-ayes.

The display of **explorative behaviours** differed between individuals and was influenced by condition. However, even though all individuals displayed highest absolute values of explorative behaviours in the enriched condition (Fig. 5), differences between the conditions were not always significant. Remarkably, both adult individuals showed more explorative behaviours in the enriched than the control condition whereas the subadult male spent much more time with exploration overall but was not influenced by condition. This suggests an effect of age. In rats, enrichment increased exploration in adult but not in young animals (Mench, 1998). Age affecting explorative behaviours, neophobia, and neophilia has also been described for several non-domestic species, and exploratory tendencies decrease in a wide range of species as individuals get older (Sherratt & Morand-Ferron, 2018).

As there were more options for enrichment interactions in the enriched than in the other conditions, the higher levels of explorative behaviours in the enriched condition seem to be intuitive. Yet, several species have been found to prefer food they have to work for over freely available treats of the same quality (e.g., common starling (*Sturnus vulgaris*): Inglis & Ferguson, 1986; brown rats (*Rattus norvegicus*): Carder & Berkowitz, 1970). As the aye-ayes frequently explored or manipulated the enrichments after no food was left, our findings indicate that the aye-ayes voluntarily interacted with the provided enrichments even though this was not necessary to fulfil their dietary requirements.

Behavioural variability of the focal animals was affected by all possible interaction terms of enrichment condition, individual, and time of day indicating that each of these factors influences BV in aye-ayes. The males tended towards higher BV in the evenings, whereas the female reduced BV over the day. This is likely associated to the amount of time she spent sleeping, which increased during the day in all conditions and plateaued at 100% from 5 pm. Like in the explorative behaviours, the subadult male did not change BV depending on condition, whereas the adults did. For the subadult male this effect is likely linked to the constantly high levels of explorative behaviours and therefore an age effect as discussed above. The adult aye-ayes showed higher BV in the enriched condition compared to the control condition but intermediate BV in the unenriched condition. An increase of behavioural diversity due to enrichment was found in armadillos (*Dasypus novemcintus;* Clark & Melfi, 2012), galagoes (*Galago senegalensis;* Clark & Melfi, 2012), small felids (*Felis viverrina* & *F. bengalensis;* Shepherdson et al., 1993), and giant pandas (*Ailuropoda melanoleuca*; Swaisgood et al., 2001). In this study, the duration of the enriched and unenriched condition (21 days each) was very short compared to the duration the animals had spent in their routine husbandry (control condition) before the beginning of this study. Therefore, the intermediate values in the unenriched condition might be caused by novelty effects implied by the change of the husbandry regime.

Conclusions

Because all behavioural indicators were influenced by at least two factors (Tab. 10), factors partly influenced each other (e.g., noise and visitors), the duration of the study was short, and we observed only three individuals, no general conclusions can be drawn from this study. Nevertheless, our study presents examples for suitable food-based enrichment and our results provide first valuable insights into the factors that may influence SB in aye-ayes.

Even though the aye-ayes at Frankfurt Zoo did not reduce the display of SB if more food-based enrichment was provided, they still seemed to benefit from the enrichment. All aye-ayes interacted with the enrichment, although this was not necessary to fulfil their dietary requirements. Behaviour variability increased in two of the three focal individuals (the adults) in the enriched condition compared to the control condition. Furthermore, we did not find evidence that the enrichment compromised aye-aye welfare.

Visitors and noise levels in front of the enclosures influenced the behaviour of the aye-ayes at Frankfurt Zoo. Both measures were weakly positively correlated with the display of SB and might have shaped aye-aye behaviour through long-term effects, e.g., because noise levels and visitor numbers depend on the time of day, so that aye-ayes might accommodate their behaviour budget to that.

Our case study should be regarded as a starting point to further investigate long-term effects of enrichment, visitors, and noise on the behaviour of aye-ayes with the goal to develop effective strategies to reduce and prevent SB. Until more data is available, we advocate the use of foraging enrichment, as the positive trends found in this study are likely to have positive effects on the welfare of aye-ayes in human care.

Tab. 10: Overview of factors influencing the behavioural indicators used in this study.

	Stereotypic behaviour	Out of sight	Explorative behaviours	Behaviour variability
Number of visitors	✓	-	-	-
Noise level	✓	✓	-	-
Time of day	✓	✓	-	✓
Enrichment condition	✓	✓	✓	✓
Individual	✓	✓	✓	✓

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Zusammenfassung

Das Fingertier (*Daubentonia madagascariensis*) ist ein nachtaktiver Lemur mit mehreren körperlichen Besonderheiten wie Nagezähnen, vergrößerten Ohren und verlängerten Fingern. Diese nutzt es für eine spezialisierte Nahrungssuchstrategie („percussive foraging“). In menschlicher Obhut zeigen Fingertiere häufig stereotype Verhaltensweisen. Daher untersucht diese Studie, ob futtermotivierte Beschäftigung, welche zu percussive foraging anregt, das Verhalten von drei im Zoo Frankfurt gehaltenen Fingertieren verändern und Anzeichen verbesserten Wohlbefindens hervorrufen kann.

Wir beobachteten die Fingertiere in drei Haltungskonditionen: Kontrolle (Standardhaltung), angereichert und nicht angereichert. Die Datenerhebung erfolgte mittels instantaneous sampling von Mai bis August 2013. Zur Bewertung der Effektivität der Beschäftigung haben wir vier Verhaltensindikatoren definiert: Auftreten stereotyper Verhaltensweisen (SB), Zeit außerhalb des Sichtbereichs, exploratives Verhalten und Verhaltensvariabilität (BV). Um Informationen über mögliche Ursachen für Verhaltensänderungen zu gewinnen, haben wir den Einfluss von fünf Faktoren (Individuum, Haltungskonditionen, Geräuschpegel, Besucher vor den Gehegen und Tageszeit) auf diese Verhaltensindikatoren geprüft.

Jeder Verhaltensindikator wurde vom Individuum und mindestens einem weiteren Faktor beeinflusst. Das Auftreten von SB korrelierte positiv mit der Anzahl der Besucher vor den Gehegen sowie mit dem Geräuschpegel. Fingertiere zeigten mehr SB an Nachmittagen der angereicherten Kondition als an Nachmittagen unter der Kontrollbedingung. Während der Mittagszeit (12:30-15:30 Uhr) korrelierte die Zeit, die die Fingertiere außerhalb des Sichtbereichs verbrachten, positiv mit dem Geräuschpegel. Ein Fingertier verbrachte in der angereicherten Kondition weniger Zeit außerhalb des Sichtbereichs als in der nicht angereicherten. Zwei Fingertiere, beide adult, zeigten in der angereicherten Kondition mehr exploratives Verhalten und die höchste BV.

Unsere Studie nennt Beispiele für geeignete Futter-basierte Beschäftigung und enthält neue Erkenntnisse über Faktoren, die SB bei Fingertieren potenziell beeinflussen. Da jedoch alle Verhaltensindikatoren von mindestens zwei Faktoren beeinflusst wurden, sich diese Faktoren teilweise gegenseitig beeinflussten und die Studiendauer sowie die Stichprobengröße gering waren, lassen sich keine allgemeinen Schlussfolgerungen über das Verhalten von Fingertieren ziehen. Zukünftige Studien sollten den Einfluss von Lärm und Besuchern auf Fingertiere vertieft untersuchen sowie effektive Strategien zur Reduktion von Stereotypien bei Fingertieren evaluieren. Da unsere Daten keine Hinweise darauf geben, dass futterbasierte Beschäftigung das Wohlbefinden von Fingertieren beeinträchtigt und gleichzeitig bei zwei beobachteten Individuen in der angereicherten Kondition eine erhöhte BV festgestellt wurde, sprechen wir uns für den Einsatz von futtermotivierter Beschäftigung aus, bis weitere Erkenntnisse vorliegen.

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