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Specifically Unspecific – Simple Devices as Feasible and Effective Enrichment for Small Mammals

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Abstract – Although enrichment is an essential part of modern zoo animal husbandry, research on effective enrichment for small mammals is scarce, albeit they are regularly kept in zoos. To develop solutions that are inexpensive, readily applicable, and adaptable for a variety of species, we investigate whether three types of simple enrichment devices (SEDs) – object, olfactory, and food-motivated – elicit positive interactions in various zoo-housed small mammal species. In this preliminary exploration study, we evaluate if amount of enrichment interactions, display of behavioral stress reactions, and display of stereotypic behaviors vary, if different types of SEDs are provided. Therefore, we observed 39 individuals of ten species, most of which are underrepresented in enrichment literature: Eastern quoll (*Dasyurus viverrinus*), round-eared elephant shrew (*Macroscelides proboscideus*), aardvark (*Orycteropus afer*), southern tamandua (*Tamandua tetradactyla*), northern Luzon giant cloud rat (*Phloeomys pallidus*), green acouchi (*Myoprocta pratti*), South African springhare (*Pedetes capensis*), aye-aye (*Daubentonia madagascariensis*), golden lion tamarin (*Leontopithecus rosalia*), and Javan mouse-deer (*Tragulus javanicus*) housed in Frankfurt Zoo, Germany. All focal individuals interacted with at least two types of SEDs and around 80% interacted with all types of SEDs, resulting in a considerable amount of time spent with the enrichment. There was a preference for food-motivated enrichment. Neither behavioral stress reactions nor stereotypic behaviors differed if different types of SEDs were present. Model selection showed that GLMs explaining enrichment interactions improved if the variable ‘individual’ instead of ‘species’ was included, suggesting that reactions towards unspecific SEDs might be more individual-driven than species-specific. Because individuals of all species chose to interact with the SEDs and we did not find behavioral indicators for stress elicited by the SEDs, we advocate for the regular provision of SEDs for small mammals in human care.

Keywords – Animal welfare, Zoo, Behavioral enrichment, Stereotypy, Animal husbandry, Multi-species approach

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Modern zoos and zoo associations continuously work on refining husbandry best practice and increasing animal welfare in their institutions (Mellor et al., 2015). In recent years, the subject area of enrichment, i.e., the provision of choice or addition of stimuli that results in improved animal welfare (de Azevedo et al., 2007), has received growing attention, with manifold enrichment devices and concepts having been developed and evaluated for a variety of species (e.g., French et al., 2018; Goswami et al., 2021; Rooney & Sleeman, 1998). Enrichment and welfare research has, however, not been distributed equally between taxa, seemingly favoring socially housed and mammalian species (Kresnye et al., 2022), while neglecting groups such as amphibians and reptiles (Burghardt, 2013; Näslund & Johnsson, 2014; Williams et al., 2009). Yet, even within Mammalia, most studies focus on charismatic large species such as apes, large carnivores, and elephants, whereas reports of small mammal species often receive less attention in the literature (Alligood & Leighty, 2015; Binding et al., 2020; Melfi, 2009; Swaisgood & Shepherdson, 2005). This might reflect the reduced application of enrichment for groups like small carnivores (Riley & Rose, 2020), nocturnal mammals (Clark & Melfi, 2012), and potentially other small mammals, and/or a publication bias (Brereton & Rose, 2022).

The number of species and individuals affected by this lack of enrichment provision and/or published research is quite high. Unfortunately, contemporary development of scientifically validated measures for these and further species seems unrealistic as confirming the effects of enrichment is time and resource-consuming (e.g., Hoy et al., 2009) and single institution studies often cannot be extrapolated due to small sample sizes and heterogenous conditions. Moreover, individuals (even within the same species) are unique in their preferences and needs (Barber et al., 2010; Boissy et al., 2007; Hosey et al., 2009), thereby differing in their responsiveness to and preferences of enrichment (Dallaire et al., 2012; Fay & Miller, 2015; Eskelinen et al., 2015). Therefore, focusing only on species-specific features without regard to individual preferences does not ensure that enrichment results in good welfare (Whitham & Wielebnowski, 2013). Opening the current focus of single-species enrichment research towards a broader scale, i.e., studying enrichment not of a particular species but for animals that share similar niches or are housed in similar conditions, could therefore be constructive: it may enhance the quality of life of many zoo-housed animals that face few changes and stimuli and have plenty of vacant access time in comparison to their wild conspecifics (e.g., Hughes & Duncan, 1988; Morgan & Tromborg, 2007; Watters, 2009). These conditions potentially lead to boredom-like states, in turn, compromising welfare (Lilley et al., 2017; Meagher & Mason, 2012; Meagher, 2018). Hence, providing these animals with varying stimuli (enrichment) and therefore opportunities to occupy their time, has the potential to increase their welfare.

To promote research on the effects of enrichment for small mammals and to develop inexpensive and intuitive solutions, we investigated whether unspecific simple enrichment devices (SEDs), such as paper rolls filled with food, novel objects, and scents elicit positive interactions, and occupy the time of various small zoo-housed mammals. We use the term SEDs as an umbrella term for various almost costless and easily applicable enrichment options that are specifically unspecific, i.e., not custom made for a species or individual. SEDs could still be of high value for small mammals, because they can add variety to enclosures. They have the further advantage that they are often available as residuals of daily zoo business and can be acquired in high numbers, even if no enrichment budget is left. Although without a close phylogenetic relationship, we categorize our focal species as "small mammals." This gives a good idea of the investigated group in distinction to other mammalian species that are the focus of most welfare research.

In practice, SEDs are occasionally given to many species, including small mammals, with the goal to provide novelty and opportunities for the animals to engage in pleasurable activities or increase species-typical behaviors (Tresz, 2007; Wooster, 1997; Young, 2003). SEDs are not typically applied within enrichment evaluation frameworks (e.g., SPIDER; Alligood & Leighty, 2015; Mellen & MacPhee, 2001), so that interactions with these enrichments remain unquantified (pers. observation, but described in the past by Barber, 2006; Mellen & MacPhee, 2001). Whenever enrichment is applied, it is essential to assure that animal welfare is not accidentally compromised (e.g., Mellor et al., 2015). Rainforest sounds, for example, led to a decrease in species-typical behavior in galagoes (*Galago senegalensis*) and sloths (*Choloepus didactylus*; Clark & Melfi, 2012). It is also important to ensure that the animals subjectively profit from the enrichment, as otherwise the act of providing ineffective enrichment might lead to a false assumption of good animal welfare. Therefore, enrichment outcomes should be evaluated through an animal-centric lens. Enrichment can be considered effective only if it does not impair welfare (indicated by, e.g., stereotypies or self-harmful behaviors), and at the same time promotes positive or improved welfare including positive affective states (e.g., play or reduction of indicators of impaired welfare) or target behaviors (e.g., species-typical behaviors or increased enclosure use; Alligood & Leighty, 2015; Mellen & MacPhee; 2001, Young, 2003).

We investigated if various small mammal species voluntarily engage with SEDs and examine possible negative effects of SEDs to determine whether SEDs should be broadly applied or if they should be used only after critical evaluation of every device. Therefore, we evaluated if amount of enrichment interactions, display of behavioral stress reactions, and display of stereotypic behaviors vary, if different types of SEDs are provided. Although not the focus of the study, we additionally explored differences in enrichment interaction at both the individual and species levels. We did so because we argue that individual rather than species differences may be better predictors of interactions with SEDs. Therefore, SEDs may be a valuable method for occupying the time of and enriching small mammals regardless of their species (under the precondition that SEDs elicit few or no behavioral stress reactions or stereotypic behaviors).

We hypothesized that most individuals would interact with the provided SEDs. To investigate the reactions of different taxa, we selected ten phylogenetically, ecologically, and behaviorally diverse small mammal species and investigated the reactions of 39 readily distinguishable individuals towards three types of SEDs: object, olfactory, and food-motivated. Until now, some studies have investigated food-based species-specific enrichments for two of our focal species and one taxon including one of our focal species (food-based enrichment for tamanduas: Eguizábal et al., 2013; Neto et al., 2020; differing enrichments for aardvarks: Hamilton et al., 2020; gum and puzzle feeders for Callitrichids: Sanders & Fernandez, 2022; Sha et al., 2016; Regaiolli et al., 2020). We could not find any scientific publications on enrichment for six of the investigated species. Therefore, gaining information on how these species react to SEDs and how small mammals react to enrichment that is not associated to food is particularly valuable.

Method

Ethical Approval

As enrichment is a standard husbandry practice and the items used in this study are regularly applied at Frankfurt Zoo, no formal approval was necessary for this study. Zoo animal husbandry is controlled by regional veterinary authorities.

Subjects

We chose focal species living in the "Grzimek house" of Frankfurt Zoo with a nocturnal and a diurnal section. Opting for a data set including small mammals of various taxonomic groups, we selected eight species with individuals that could be easily distinguished by the observer (MG) according to size, coloration patterns, sexual dimorphism, individual characteristics (e.g., tail length, scars), and of which at least three specimens were present. The focal species were: Eastern quoll (*Dasyurus viverrinus*), round-eared elephant shrew (*Macroscelides proboscideus*), aardvark (*Orycteropus afer*), southern tamandua (*Tamandua tetradactyla*), northern Luzon giant cloud rat (*Phloeomys pallidus*), aye-aye (*Daubentonia madagascariensis*), golden lion tamarin (*Leontopithecus rosalia*), and Javan mouse-deer (*Tragulus javanicus*). We included two further species, because individuals of these species were co-housed with other focal animals and interacted with the SEDs. These were: green acouchi (*Myoprocta pratti*; with *L. rosalia*) and South African springhare (*Pedetes capensis*; with *O. afer*). In this way, we were able to enlarge our data set concerning the number of individuals (39), as recommended by Swaisgood and Shepherdson (2005), species (10), and total number of observation units (461). The number of individuals and observations varied between species (Table 1). One individual aardvark was excluded from analyses because it was never active during observation units and tended to sleep all day in a den, likely being unaware of the enrichment device unlike other, co-housed individuals. All focal animals were born in zoos and accustomed to their enclosures when observations commenced.

Table 1

Focal Individuals

Species	Individual ID	Sex	Age	Observation Units				Comments
				OB	OL	FM	Total	
Eastern quoll (*Dasyurus viverrinus*) max. age: 6.8 years	Anton	m	y/a	6	6	6	18	
	Puenktchen	f	y/a	6	6	6	18	
	Mila	f	a	5	6	6	17	
Round-eared elephant shrew (*Macroscelides proboscideus*) max. age: 8.5 years	Male_Xhaus	m	a	2	2	2	6	
	Female_Xhaus	f	y	2	2	2	6	
	Male_Affen	m	a	2	2	2	6	
	Female_Affen	f	a	2	2	2	6	
Aardvark (*Orycteropus afer*) max. age: 29.75 years	*Ernst*	*m*	*y*	*0*	*0*	*0*	*0*	*excluded*
	Ermine*	f	y	1	0	0	1	repeatedly oos
	Lotte	f	y	2	1	2	5	repeatedly oos
Southern tamandua (*Tamandua tetradactyla*) max. age: 16.5 years	Pepita	f	a	8	7	7	22	
	Pancho	m	y	2	2	2	6	
	Evita	f	a	5	4	4	13	
	Paula	f	a	5	5	6	16	
	Yoda	m	y	6	4	6	16	
Green acouchi (*Myoprocta pratti*) max. age: 14.75 years	MyoPra_Male	m	y/a	2	2	2	6	
South African springhare (*Pedetes capensis*) max. age: 20 years	Mia	f	y/a	4	5	4	13	
	Hassan	m	y	2	2	2	6	
Northern Luzon giant cloud rat (*Phloeomys pallidus*) max. age: 13.5 years	Borat	m	y/a	6	5	4	15	
	Bora	f	y/a	5	6	6	17	
	PhlPal_Aug13	f	y	2	3	3	8	
	PhlPal _Mar14	f	y	2	3	3	8	
	PhlPal _Nov14	f	y	4	4	4	12	
	PhlPal _Apr15	m	y	4	4	4	12	
	PhlPal _Aug15	m	y	1	2	2	5	displacement
Aye-aye (*Daubentonia madagascariensis*) max. Age: 23.25 years	Malala	m	a	6	6	6	18	
	Kimala	m	y	6	6	6	18	
	Vintana	m	y	5	4	2	11	
	Kintana	f	a	2	2	2	6	
Golden lion tamarin (*Leontopithecus rosalia*) max. age: 31.5 years	Alfons	m	y	7	7	7	21	
	Antonia	f	y	7	7	7	21	
	Anja	f	Y	7	7	7	21	
	Albert	m	y	4	4	4	12	
	Annabell	f	y	7	7	7	21	
	Alberto	m	y	2	2	2	6	
Javan mouse-deer (*Tragulus javanicus*) max. age: 14 years	TraJav_Male	m	y/a	6	6	6	18	
	TraJav_Female	f	y/a	6	6	6	18	
	TraJav_Jul14	f	y	2	2	2	6	
	TraJav_Dec14*	m	y	1	0	0	1	displacement
	TraJav_Oct15	f	y	2	1	2	5	displacement
Total	39 (40)			156	152	153	461	

Note. Observations with OB = object enrichment, OL = olfactory enrichment, and FM = food-motivated enrichment. Max. age = maximum age reached by the species after Puschmann et al. (2009) and Encyclopaedia of Life, www.eol.org, for aye-ayes and quolls; age = age group (y = young, first thirds of the max. lifespan; a = adult, second two thirds of max. lifespan; y/a = animals that changed age categories during observations); sex (m = male; f = female); oos = out of sight continuously for 20 min after enrichment was placed in the enclosure, so that the respective observation units were excluded for this individual, displacement = move into another enclosure or zoo that could not be included in this study. For individuals highlighted in gray no full data set could be obtained, * marks individuals that could not be observed with all enrichment types, italics highlight individuals that could never be observed and were excluded from the study.

For further analyses, we classified focal individuals into species and age groups (young, adult; Table 1); age has been shown to be related to the prevalence of stereotypic behaviors in several species (Mason, 1993; Vickery & Mason, 2004; Würbel, 2006). Animals in the first third of the maximum life span of the species were classified as "young," animals in the last two thirds were classified as "adult" (life span after Puschmann et al., 2009 and Encyclopaedia of Life, www.eol.org, for aye-ayes and quolls).

Materials and Procedures

We investigated the reaction of the focal animals towards three different types of enrichment: object, olfactory, and food-motivated (Figure 1). Enrichments were placed randomly on the enclosure floor. Irrespective of the number of present focal individuals, we provided three SEDs of the same type per enclosure and observation unit to guarantee that all enrichment interactions could be observed, even if several focal individuals were present. It was possible that several individuals interacted with the same item simultaneously. Given that focal individuals were born in different zoos, have changed enclosures over time, and were taken care of by various keepers, it was not possible to determine which individuals had experience with the provided SEDs (or similar enrichment devices) before the observations for this study. During the study, focal animals received the investigated SEDs only during observations.

Figure 1

Simple Enrichment Devices (SEDs) Used in This Study

Note. From left to right: object SED (stone) in the enclosure of round-eared elephant shrew, olfactory SED in preparation (pieces of wood placed in spice powder), and food-motivated SED (paper roll filled with paper containing insect larvae) in enclosure of southern tamandua. Photos by MG.

Based on morphological differences and varying food preferences of the focal species, we slightly adapted the SEDs depending on species, if necessary. The object enrichment consisted of three stones (5-10 cm length, 5-8 cm width, 3-5 cm height, natural stones) that we distributed in the enclosures. After every observation unit, stones were washed under running water without soap and dried to prevent transfer of odors and dirt. Olfactory enrichment consisted of three small pieces of wood (3-7 cm length, 1-2.5 cm diameter except for mouse-deer: 5-7 cm diameter) that were placed for several days in curry, sweet chili, and cinnamon powder, respectively. We used differing spices to avoid testing preferences for one certain flavoring. To prevent ingestion and potential choking, we used slightly enlarged pieces of wood for Javan mouse-deer. Although we could not test this, we assume the smells were detectable for all focal animals, as most focal individuals sniffed the enrichments during observations. The scents could be detected with human sense of smell after finalization of an observation unit. Food-motivated enrichment consisted of three paper rolls (10 cm length, except for tamanduas: 25 cm length) filled with paper containing living mealworms (larvae of *Tenebrio molitor*) for quolls, elephant shrews, and tamanduas; three paper rolls filled with paper containing nuts for springhares, giant cloud rats, acouchi, aye-ayes, and golden lion tamarins; three paper rolls filled with herbs for Javan mouse-deer and one perforated plastic box (cylindrical, length 30 cm, diameter 21 cm) filled with living larvae of *Zophobas morio* for aardvarks to prevent the ingestion of paper. The food was given in small amounts as it was an addition to the usual diet and therefore often depleted in course of an observation unit. We used the same objects for all observations and removed them immediately after observations, however, olfactory and food-motivated enrichments were never reused and were removed by keepers at the next cleaning.

Data Collection

We performed a total of 461 observations on 39 focal individuals of 10 small mammal species (observations for [number of individuals]: eastern quolls [3] = 53, round-eared elephant shrews [4] = 24, aardvarks [2] = 6, southern tamanduas [5] = 73, green acouchi [1] = 6, South African springhares [2] = 19, northern Luzon giant cloud rats [7] = 77, aye-ayes [4] = 53, golden lion tamarins [6] = 102, Javan mouse-deer [5] = 48, Table 1). Observations were carried out by MG from August 1, 2014, to January 31, 2016, in Frankfurt Zoo, Germany.

Observations of 60 min started at approximately 11:00 h or 15:30 h. To minimize the impact of feeding on enrichment response, this time scheme ensured that animals could be observed during hours of activity (nocturnal species were housed on reversed light-cycle), observations did not coincide with the feeding schedule, and animals were not hungry as they received food two to three hours prior. Our goal was to observe every individual with every type of SED at least once in the morning and in the afternoon, leading to a minimum of six observation units per individual. To prevent habituation to the provided SEDs in large groups, group-housed individuals and species in mixed-species exhibits were observed simultaneously. However, not all members of one species were necessarily housed in one continuous group. Due to births, tensions in groups, planned or unplanned enclosure moves, or other management reasons, group compositions changed often and even between observations of focal individuals. We did not have any influence on changing group compositions. We aimed at gaining a full data set for all focal animals, but we preferred collecting more data on the other group members during group observations over not collecting additional data to have the same number of observations for all focal individuals. This, and sometimes inactivity (see below), made it such that some co-housed focal individuals were observed more than six times (Table 1).

As we aimed to compare several species and had to find broad behavior definitions fitting them all, we decided to work with one-zero sampling (Lehner, 1998). We used a sample interval of 15 s for the interaction with SEDs, display of stereotypic behavior, and display of behavioral stress reactions (Table 2). One-zero sampling combined with the simple ethogram has the advantage that high reliability can be obtained as correct sampling is comparatively easy (Crockett & Ha, 2010; Engel, 2004; Rhine & Flanigon, 1978). In Frankfurt Zoo, neither staff nor visitors must be filmed as to protect personal information. Because the enclosures have complex shapes with large visitor windows, several levels, many hiding places, and partly a reversed light cycle, videotaping that covered whole enclosures and allowed for individual distinction was not possible under this premise. Therefore, we were not able to calculate intra-observer reliability. Yet, the observer was trained in behavioral observations of zoo animals and knew all focal species from working with them. Furthermore, she performed preliminary observations (as recommended by Crockett & Ha, 2010) employing the one-zero technique with random enclosure furniture representing enrichment. During data collection, we always used three SEDs at a time independent of the number of focal individuals. This approach allowed the recording of all interactions with the SEDs while scanning for display of stereotypic behavior and behavioral stress reactions even in medium-size groups of active focal species. Besides one-zero sampling, we noted behavior patterns displayed during enrichment interactions ad libitum (Table 3).

Observations started three minutes after the SEDs were placed within the enclosures. We made sure not to observe the same focal animals on successive days and used a pseudo-randomized observation schedule. Initially, the object enrichment (stones) was intended to serve as a control condition. Due to the high number and intensive interactions of focal animals with the stones, we decided to work with a cross-validation approach by comparing enrichment devices. Because of the pseudo-randomized setting, differences in number of interactions with the SEDs, behavioral stress reactions, and display of stereotypic behaviors should be explained by effects evoked by the enrichment. If individuals were continuously out of sight for 20 min after enrichment was placed in the enclosure, we excluded the respective observation unit for this individual from analyses, as it remained unclear whether the individual had noticed the presence of enrichment. With few exceptions this occurred only in aardvarks (Table 1), observations were repeated several days later.

Table 2

Ethogram for All Focal Species

Behavior	Definition
Enrichment interaction	Every behavior directed towards the SED and displayed in a maximum distance of two body lengths of the focal individual from the SED. We chose two body lengths after preliminary observations in which some animals tended to observe the enrichment first from a radius that was a little larger than their body length.
Behavioral stress reactions	Alarm calls, flight response from an SED, paralysis, trembling, protruding eyes, stroking hair. [No behavioral stress reactions were observed during this study.]
Stereotypic behavior	Invariant, repetitive behavior patterns without obvious goal or function (Mason, 1991a, 1991b). Behavior patterns and display locations in enclosures were defined for focal animals individually after preliminary observations.

Statistical Analyses

We conducted all statistical evaluations and several of the graphical visualizations using *R* x64 v4.0.3 (R Core Team, 2019) within *Rstudio* v1.3.1093 (Rstudio Team, 2016). For visualization and data set conversion, we generated boxplots and scatterplots with the *R* packages *ggplot2* v3.3.3 (Wickham, 2016) and *gridExtra* v2.3 (Auguie & Antonov, 2017). Via the *R stats* v4.0.3 (R Core Team, 2019), and *car* v3.0-11 (Fox & Weisberg, 2019) packages, we used Poisson generalized linear models (GLMs) and analysis of variance (ANOVA) tables (Wald χ^2 test (type II)) to test the influence of the preselected parameters. We chose GLMs as they are a comparatively simple approach to multi-level models or generalized linear mixed models (GLMMs), but still appropriate to answer our research questions and are therefore a good compromise between model complexity and depth of information provided by our data set.

Residual diagnostics were carried out with the diagnostic plots of the *R* package *DHARMa* v0.4.1 (Hartig, 2019). We conducted two models with the response variables ‘enrichment interactions’ (count data) and ‘stereotypy’ (count data) to evaluate the effect of the enrichment items on small mammals. All predictor variables in all models in this study were categorical. Behavioral stress reactions were excluded from analysis, as they were never observed during this study.

Stepwise model selection including all five predictor variables (individual [n = 39], species [n = 10], type of SED [food, object, scent], time of observation [morning, afternoon], age group [young, adult]) was achieved by GLM comparison utilizing three independent approaches: ANOVA (type I; R package stats v4.0.3 (R Core Team, 2019)), the corrected Akaike information criterion (AICc; Burnham & Anderson, 2010), and McFadden’s pseudo-R^2 (McFadden, 1979). In general, every model was categorically compared to the null model, where the predictor = 1. The model with the lowest AICc (Δ AICc $\leq$ -2) offers the best fit in comparison to the other models. If Δ AICc = [-2, 2], we selected the more comparable model. We chose the AICc as it corrects for small sample sizes (Burnham & Anderson, 2010). AICcs were calculated with the *R* package *MuMIn* v1.43.17 (Bartoń, 2019), whereas McFadden’s pseudo-R^2 was computed with the *R* package DescTools v0.99.42 (Signorell et al., 2021). As we were specifically interested in effects of the individuals, we included the factor ‘individual’ as a fixed, not a random effect. In two models we defined ‘species’ and ‘individual’ as a nested fixed effect (Table 4, EI B & EI D). We used a significance level of 5% (α = .05) and adjusted significance levels with Bonferroni correction if indicated.

After comparing different GLMs, we excluded two variables from our analysis: *time of observation* [morning or afternoon] and *age group* [young and adult] as they had no predictive power regarding the animals’ reactions towards the SEDs. Due to rare observations of stereotypic behaviors, affected GLMs suffered from zero-inflated data (Figure 2). Therefore, we chose the less complex GLM with the response variable ‘stereotypic behavior’ to accomplish GLM-based comparisons despite the values used for model selection (Table 4). The zero-inflated stereotypy data also caused model overfitting in GLMs including fixed effects and could not be executed with the utilized algorithms.

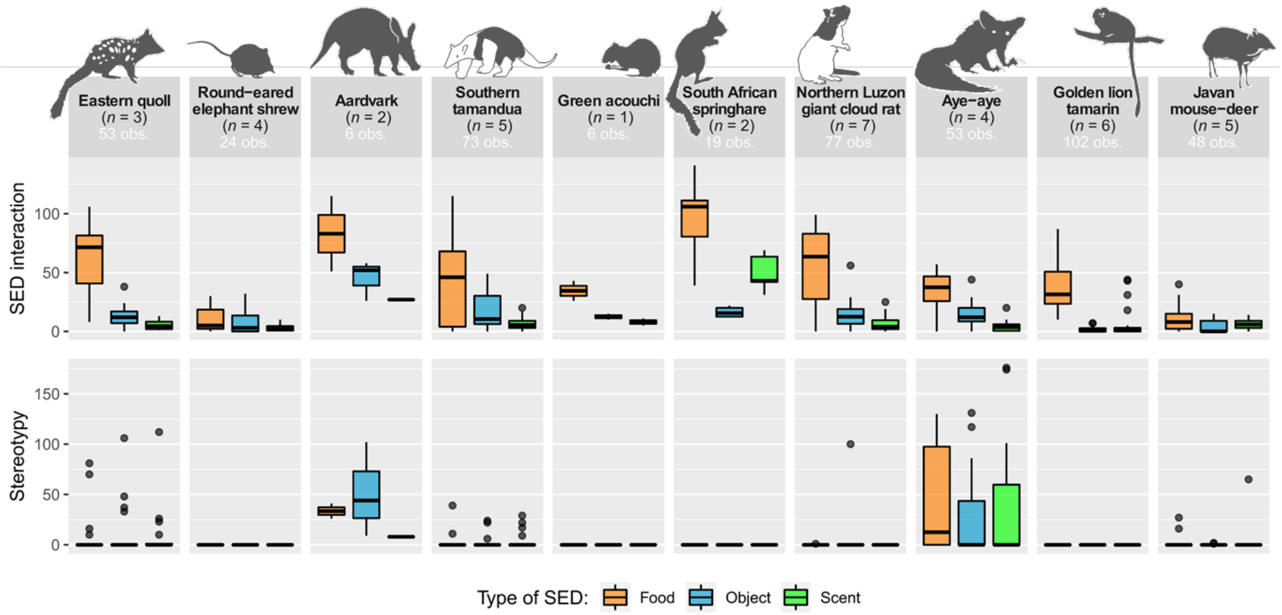
To account for our heterogenous data set and small numbers of focal individuals in some species, we repeated statistical analysis with data subsets excluding species with two or less individuals (aardvarks, springhares, green acouchi), individuals with one observation unit only (aardvark “Ermine”, Javan mouse-deer “TraJav_Dec14”), and both (Supplementary material 1-6).

Results

The number of individuals varied between species, as did the number of observations per individual (Table 1, Figure 2). Due to repeated inactivity (2/2 aardvarks) or displacement (1/7 northern Luzon giant cloud rats & 2/5 Javan mouse-deer), it was not possible to gain a full data set (6 observation units) for five focal animals (12.8%). Further, one aardvark could never be observed and had to be excluded from the study. Most focal individuals (61.5%) were observed more than six times e.g., due to changes in group composition and the need to gain a full data set for other group members. Nevertheless, we found that the results of all statistical analyses were stable when applying reduced data subsets (excluding species with two or less individuals, individuals with one observation unit, and both, Supplementary material 1-6).

Figure 2

Enrichment Interactions and Display of Stereotypic Behavior per Species and Type of Simple Enrichment Device (SED)



Note. Boxplots for counts of sample intervals with SED interactions and display of stereotypic behavior (‘Stereotypy’) per species (gray vertical columns) and type of SED (color code) in a 60 min interval (duration per observation unit). The maximum possible count for SED interactions and display of stereotypic behavior is 240 (sample interval of 15 s for 60 min). For every species, we noted sample size of individuals (*n*) and number of observation units (obs.).

Enrichment Interaction

In total, we recorded 9,541 intervals with SED interactions during 461 observation units. Ways of interacting with the SEDs differed by species and SED (Table 3). One Javan mouse-deer was observed engaging with olfactory enrichment and one aardvark with object enrichment only (Table 1). All other focal individuals were observed interacting with every type of SED at least once and interacted with at least two types of SED; 31 individuals (79.5%) interacted with all types of SED. Four individuals (10.3%) never interacted with object enrichment (1/4 round-eared elephant shrews, 1/6 golden lion tamarins, 2/5 Javan mouse-deer), one golden lion tamarin (2.6%) never interacted with olfactory enrichment and one aye-aye never with food-motivated enrichment. There was an overall tendency that scent enrichment elicited the least reactions whereas food-motivated enrichment led to most SED interactions (Figure 2).

The predictors 'species' and 'individual' each influenced the interaction with SEDs but were highly nested variables. Model selection revealed that the GLMs including only 'species' as a predictor ('EI A'; EI = GLM with response variable 'enrichment interaction') were surpassed by the models including 'individual' (Table 4). We chose 'EI C' (predictors: SED and individual) as the best fitting model as it is less complex than GLMs including nested fixed effects ('EI B' and 'EI D'), although holding similar explanatory power. Analysis of variance showed that the individual as well as the type of SED had significant effects on enrichment interactions (Table 5).

Table 3

Behavioral Patterns Displayed During Enrichment Interactions

Species	Enrichment	Sniffing	Licking	Gnawing	Chewing	Carrying around (in mouth)	Ripping	Scratching	Percussive foraging*	Manipulating while holding in claws	Touching or carrying with hands	Pushing around	Digging in	Climbing on SED	Resting on SED	Watching
Eastern quoll (*Dasyurus viverrinus*)	Object	x						x								
	Olfactory	x										x				
	Food	x	x				x					x				
Round-eared elephant shrew (*Macroscelides proboscideus*)	Object	x												x	x	
	Olfactory	x														
	Food	x														
Aardvark (*Orycteropus afer*)	Object	x										x	x			
	Olfactory	x										x	x			
	Food	x	x									x				
Southern tamandua (*Tamandua tetradactyla*)	Object	x						x								
	Olfactory	x						x		x		x				
	Food	x					x	x		x						
Green acouchi (*Myoprocta pratti*)	Object	x		x												
	Olfactory	x		x									x			
	Food	x		x		x										
South African springhare (*Pedetes capensis*)	Object	x		x								x	x			
	Olfactory	x		x									x			
	Food	x		x		x				x		x	x			
Northern Luzon giant cloud rat (*Phloeomys pallidus*)	Object	x		x								x				
	Olfactory	x	x	x		x										
	Food	x	x	x	x	x										
Aye-aye (*Daubentonia madagascariensis*)	Object	x				x			x				x			
	Olfactory	x	x	x	x	x										
	Food	x	x	x	x				x							
Golden lion tamarin (*Leontopithecus rosalia*)	Object		x								x	x				
	Olfactory		x		x						x					
	Food	x	x		x		x				x					x
Javan mouse-deer (*Tragulus javanicus*)	Object	x														
	Olfactory	x	x													
	Food	x														

Note. Description of behavioral patterns displayed by focal species while interacting with different types of SEDs. The behaviors in this table were not quantified during observations but noted after observation units. Sniffing: Increased nose movements or sniffing sounds while directed towards and in distance of max. two body lengths of SED. Licking: Touching SED with tongue. Gnawing: Chewing on enrichment with specialized rodent(like) incisivi, usually includes destruction of SED. Chewing: Having (parts of) SED in mouth with mouth movements. Carrying around: Transporting SED in hands or mouth. Ripping: Destroying SED by fixing one part and pulling another part with hands or mouth. Scratching: Touching SED with hands or claws in a (repeated) movement along the surface of SED. Percussive foraging: Foraging technique of aye-ayes; tapping on surfaces with specialized fingers while listening to the sound emitted by the tapping. Manipulating while holding in claws: Moving, sniffing on, licking, gnawing, chewing, or otherwise interacting with SED while holding in claws. Touching or carrying with hands: Touching SED briefly with hands (e.g. to sniff hands afterwards), holding it or carrying it around while held in hands. Pushing around: Moving SED on the floor with body, e.g. snout or hands. Digging in: Covering SED in substrate. Resting on SED: Resting behavior, e.g. closing of eyes, yawning, resting of head, while sitting on SED. Watching: Observation of SED while directed towards and in distance of max. two body lengths of SED.

Table 4

GLM Selection Analysis

Name	Model	Analysis of Deviance Table					AICc	McFadden's pseudo-R^2	adjusted McFadden's pseudo-R^2
		Resid. Df	Resid. Deviance	df	Deviance	*p*-value			
GLMs with the response variable 'Enrichment interaction'									
EI 0	Null model	460	13250.3				14952.4	.0	-.0001338
EI A	SED+sp	449	5854.7	11	7395.6	<.001	7579.5	.4946766	.4930713
EI B	**SED+sp/ind**	**420**	**4489.1**	**29**	**1365.6**	**<.001**	**6279.4**	**.5860163**	**.5805315**
EI C	**SED+ind**	**420**	**4489.1**	**0**	**.0**		**6279.4**	**.5860163**	**.5805315**
EI D	SED+age+time+sp/ind	418	4488.9	2	.2	.913	6284.1	.5860285	.5802761
GLMs with the response variable 'Stereotypic behavior'									
ST 0	Null model	460	14740.3				15047.3	.0	-.0001329
ST A	SED+sp	449	8208.3	11	6532.0	<.001	8538.0	.4341553	.4325601
ST B	SED+ind	420	3168.2	29	5040.1	<.001	3563.5	.7691490	.7636988
ST C	SED+age+time+ind	418	2610.3	1	248.8	<.001	3010.4	.8062286	.8005126

Note. Note. GLM selection analysis with the response variables 'enrichment interaction' and 'stereotypic behavior' based on analysis of deviance table, the corrected Akaike's information criterion (AICc), and the (adjusted) McFadden's pseudo-R^2. All *p*-values '< .001' equal $< 2.2e^{-16}$. The best fitting model based on the used values is printed in bold whereas the finally chosen GLM is highlighted in gray. Age = age group, (young or adult); EI = names for GLMs with response variable 'enrichment interaction'; ind = individual; SED = simple enrichment devices; sp = species; ST = names for GLMs with response variable 'stereotypic behavior'; time = time of observation (morning or afternoon).

Table 5

Analysis of Variance Tables

Response Variable ▶	Enrichment Interaction				Stereotypic Behavior			
Predictor Variable ▼	Wald $\chi 2$	df	*p*-value		Wald $\chi 2$	df	*p*-value	
SED	4469.6	2	< .001	***	3.7	2	.159	ns
Individual	3162.1	38	< .001	***	2813.8	38	< .001	***

Note. Type II analysis of variance tables (ANOVA) for the best fitting GLMs for the response variables 'enrichment interaction' and 'stereotypic behavior'. The significance code of three asterisks marks a highly significant *p*-value, 'ns' stands for a non-significant result. All *p*-values '< .001' equal $< 2.2e^{-16}$, adjusted significance level after Bonferroni correction is $\alpha_j = .025$. SED = simple enrichment devices.

Behavioral Stress Reactions and Stereotypic Behaviors

No individual was observed to show behavioral stress reactions after SEDs were put into the enclosures. In 3,017 recorded sample intervals, 11 of the 39 focal animals (28.2%, Table 6) displayed stereotypic behaviors. Round-eared elephant shrews ($n = 4$), green acouchi ($n = 1$), South African springhares ($n = 2$), and golden lion tamarins ($n = 6$) did not display stereotypic behaviors; aardvarks ($n = 2$) and aye-ayes ($n = 4$) showed the highest rates of stereotypic behaviors (Figure 2).

Model selection revealed that the GLMs best explaining ‘display of stereotypic behaviors’ did not include ‘species’ as variable (as did ‘ST A’; ST = GLM with response variable ‘stereotypic behavior’). We chose the GLM ‘ST B’, as it is less complex and less susceptible to potential overfitting than the model ‘ST C’ (cf. section ‘statistical analyses’), although holding only marginally inferior explanatory power (Table 4). An ANOVA showed that the individual had a significant impact on the quantity of stereotypic behaviors whereas present type of SED had no effect (Table 5).

Table 6

Display of Stereotypic Behaviors by the Focal Animals

Species	Type of stereotypic behavior	Number of individuals displaying stereotypic behavior
Eastern quoll	Pacing	3 (of 3)
Round-eared elephant shrew	None observed	0 (of 4)
Aardvark	Pacing	2 (of 2)
Southern tamandua	Pacing	1 (of 5)
Green acouchi	None observed	0 (of 1)
South African springhare	None observed	0 (of 2)
Northern Luzon giant cloud rat	Pacing	1 (of 7)
Aye-aye	Pacing, circling	3 (of 4)
Golden lion tamarin	None observed	0 (of 6)
Javan mouse-deer	Pacing	1 (of 5)

Discussion

Whether enrichment is considered as being effective depends on the goals it was designed for. Possible goals include reduction of stereotypic behavior, increase of physical activity, or stimulation of species-specific behavior (Bloomsmith et al., 1991; Mellen & MacPhee, 2001; Young, 2003). In this study, we used simple enrichment devices (SEDs), i.e., resource efficient and specifically unspecific enrichment options, with the goal to occupy time of zoo animals by eliciting enrichment interactions rather than behavioral stress reactions or stereotypic behaviors. Small mammals are often kept in comparatively barren indoor enclosures (as standards are generally lower, reflected for example in the German Expert Opinion on Minimum Requirements for the Husbandry of Mammals compiled by the BMEL, Federal Ministry of Food and Agriculture, 2014) and do not receive the same attention as larger species (Alligood & Leighty, 2015; Binding et al., 2020). The provision of varying stimuli and opportunities for interaction via SEDs might therefore be beneficial for many small mammals. This broad approach is not necessarily in line with the current best practice to develop enrichments that meet species-specific needs (Mellen & MacPhee, 2001; Mellor et al., 2015). Compared to species-specific enrichments, SEDs are probably also less effective. Nevertheless, if applied for many small mammal species, SEDs might help to better meet the needs of many individuals, especially if there are no or few proven species-specific enrichment options available.

Because small mammal species are generally understudied, we aimed to include several diverse small mammal species in this study. Due to restrictions of the zoo setting, sample sizes for most focal species were limited and observation units were not equally distributed between taxa. We share these limitations with other behavioral zoo studies investigating several species (e.g., Clark & Melfi, 2012, $n_{\text{total}} = 6$, species = 3; Williams et al., 2021, $n_{\text{total}} = 27$, species = 8), or examining the influences of enrichment on the small mammals observed in this study (Eastern quoll: none found (nf); round-eared elephant shrew: nf; aardvark: Hamilton et al., 2020, $n = 4$; southern tamandua: Eguizábal et al., 2013, $n = 5$; Neto et al., 2020, $n = 6$; green acouchi: nf; South African springhare: nf; northern Luzon giant cloud rat: nf; aye-aye: nf; golden lion tamarin: Sanders & Fernandez, 2020, $n = 2$; Rapaport, 1998, $n = 4$; Javan mouse-deer: de Figueiredo et al., 2021, $n_{\text{zoos}} = 10$). Nevertheless, these small samples potentially lead to biased results caused by behavioral peculiarities of single focal individuals, group dynamics, or other factors. To address and mitigate biases, we implemented several measures: (1) We repeated observations and performed them at different times of day to integrate varying influences of unknown factors. (2) We included several factors ('age,' 'time of day,' 'species,' and 'individual') in our statistical models. Although we considered group size, we did not include it as a factor due to dynamic changes in groups across species, substantial differences of natural group sizes of the focal species, to prevent triple nestedness of the factors 'individual' / 'group' / 'species' in several cases, and to reduce model complexity. There might be an influence of group dynamics confounding with the factor 'species.' We argue that our results are still valid as most species were housed in several groups, group compositions fluctuated, and several individuals could interact with SEDs at the same time. Multi-level models would be a good approach to further investigate social influences on enrichment in groups. (3) To double-check our results, we repeated statistical analyses after the exclusion of three data subsets (species with two or less individuals, individuals with one observation unit only, and both). Thereby, we confirmed that our results were not measured because of a bias caused by species with very low numbers of individuals alone, as the results did not change. Albeit our models result in high AICc values, which could imply a less favorable trade-off between model fit and data complexity, it is important to interpret the AICc values in the context of alternative models. The AICc is designed to determine which model fits a limited dataset best among a list of potential models and thus is a relative measure of the GLM performance (Burnham & Anderson, 2010).

Ensuring quality of observations poses a challenge if focal species are as diverse as ours. Therefore, we opted for simplicity in all aspects of the study. For data collection we chose one-zero sampling that allows easy recording and can result in high measures of inter-observer reliability after a brief learning phase (Crockett & Ha, 2010; Engel, 2004; Rhine & Flanigon, 1978), as calculating intra observer reliability was not feasible. Moreover, we used the same ethogram for all species and had all observations performed by the same trained observer (MG). In addition, we aimed to minimize observational error by excluding units for inactive individuals 20 minutes after the start of the unit, to account for uncertainty about the individual's awareness of the presence of the enrichment. Although we repeated the observations, if possible, this could bias data towards higher engagement with SEDs. However, inactivity during observation units occurred very clustered and almost exclusively in aardvarks (for other animals that were inactive during observation units, these could be repeated, Table 1). As we computed all statistical tests excluding species with two or less focal animals (including aardvarks), and results did not change, we assume that effects on the results of the study are negligible.

Due to unanticipated high levels of interaction with the intended control condition (object enrichment/stones), we did not obtain baseline levels for display of stereotypic behaviors. Therefore, we cannot draw conclusions on how SEDs influenced levels of stereotypies. Nonetheless, we can compare stereotypy levels in the presence of different types of SEDs. Because we never observed behavioral stress reactions in course of the study, we can furthermore be sure that the SEDs did not elicit those in our focal individuals during the observation period. In addition, we observed numerous interactions with different types of SEDs throughout the focal species and recorded displayed behavior patterns. For six of the species, this is the first research on their enrichment use. Overall, we were able to gain information on enrichment interactions and display of stereotypic behaviors and present the first data for several understudied small mammal species.

Interactions with Simple Enrichment Devices (SEDs)

Most focal species in this study are social and usually housed in groups or pairs. Therefore, as it was the best option to prevent strong habituation to SEDs in large groups and observe real-(zoo)-life effects elicited by SED, we observed group housed individuals simultaneously even though this leads to data that is not completely independent. Given that we were unable to observe interactions with more than three items at the same time, but still needed to observe all enrichment interactions in groups, we provided three SED items per observation unit, independent of group size. This allows monopolization of an SED, potentially biasing the data towards a lower number of individuals with opportunities for enrichment interaction. Furthermore, some animals destroyed scent or food enrichments (gnawing until not visible anymore), carried them out of sight, or buried them so that further observations of enrichment interaction were not possible for the respective observation unit. Yet, all focal individuals that we observed with all three types of SEDs interacted with at least two types, about 80% (31/39) interacted with all offered types of SEDs. The high numbers of interactions with the SEDs across focal species indicate that SEDs have large potential to evoke positive affective states, as all animals had an equal opportunity to not interact with SEDs. Used frequently for prolonged periods, SEDs might therefore increase the quality of life of many individuals by occupying access time and offering behavioral opportunities (Mason et al., 2007). To better understand the needs of small, zoo-housed mammals, and to improve husbandry systems, future studies should investigate if the long-term provision of varying SEDs influences the welfare of zoo animals.

Species tend to react to SEDs with different behavior patterns (Table 3). Yet, the number of interactions with SEDs was better explained by the individual rather than the species, as shown by model selection (Table 4): Despite the higher model complexity due to more factor levels in 'individual' than in 'species,' models including the factor 'individual' led to higher relative model quality measured independently by the AICc, McFadden's pseudo-R^2, and adjusted McFadden's pseudo-R^2. This might indicate that whether unspecific SEDs are effective in occupying an animal's time and thereby possibly promoting animal welfare depends on individual preferences and cannot necessarily be predicted by observed reactions of other individuals or experiences made with the species. Future hypothesis-driven studies should investigate how individuals of different species differ in their reactions to enrichments and whether species or other factors as husbandry conditions explain differences. Therefore, sufficient individuals of several groups, preferably housed in multiple zoos (Swaisgood & Shepherdson, 2005, 2006), should be investigated with the same protocol for all species, so that data are comparable (Vickery, 2006). Although we did not observe behavior without presence of SEDs and therefore cannot conclude whether SEDs are beneficial, we observed that most focal individuals chose to interact with SEDs. Furthermore, we did not find signs that small mammals suffer from the provision of SEDs. The voluntary interaction of focal individuals with SEDs suggests that small mammals might profit from SEDs. This aligns with results of meta-analyses, which have found that provision of enrichment can reduce display of stereotypic behaviors (Shyne, 2006; Swaisgood & Shepherdson, 2005, 2006). Therefore, the use of SEDs should be considered for small mammals, especially if no other enrichment concepts are in place. It is likely that, due to effects of novelty (e.g., Mench, 1998; Trickett et al., 2009; Young, 2003) and freedom of choice (e.g., Kurtycz, 2015; Leotti et al., 2010; Morgan & Tromborg, 2007), the more diverse the SEDs that are provided, the higher the probability to elicit positive affective states in various individuals. As group dynamics and presence of visitors have been shown to influence behavior in several species (Jones et al., 2021; Miller & Mench, 2005; Wood, 1998), more work needs to be done on how these and other factors affect interaction with SEDs in small mammals.

Effects of Simple Enrichment Devices (SEDs) on Stereotypic Behaviors and Behavioral Stress Reactions

We did not record baseline levels of stereotypic behaviors. Although this is not optimal, the comparison between the enrichment conditions still yields information on the effects of different types of SEDs on stereotypic behaviors and behavioral stress reactions. As we defined stereotypic behavior patterns of all focal individuals before beginning of observations without SEDs present and no new stereotypies were observed during the study, SEDs do not seem to trigger the development of stereotypies. Furthermore, the levels of behavioral stress reactions and display of stereotypic behaviors did not differ between conditions so that there is no indication that a certain type of SED evokes these behaviors more strongly than another type. Instead, stereotypic behaviors could be explained individually (Table 5). Because stereotypies can emancipate from their original stimuli (Mason, 1991a, 1991b), the stereotypies displayed by the focal animals had therefore probably either emancipated before the beginning of the study or a lack of stimuli provided by the SEDs was not their initial cause, or both. Even though this was not investigated in this study, we believe that providing SEDs will not cause the development of abnormal repetitive behaviors, but may in fact prevent them (Mason et al., 2007; Ödberg, 1987; Würbel et al., 1998). Studies investigating the levels of abnormal behaviors in different husbandry systems are needed to identify the causes for stereotypies in zoo-housed small mammals and develop ways to improve them.

Although we did not observe behavioral stress reactions elicited by the SEDs used within this study, unwanted impacts can never be out ruled completely (Hare et al., 2007). Therefore, we advocate to monitor the first reactions towards new SEDs and to remove the items if animals seem to be scared or if dangerous situations arise (e.g., the attempt of one Javan mouse-deer to swallow olfactory enrichment made us increase the size of the wood pieces).

Conclusions

To the best of our knowledge, this is the first study to evaluate the reactions of 39 individuals of ten understudied small mammal species to various types of SEDs. Although the SEDs investigated in this study were not designed to meet species-specific needs and cannot replace adequate enclosures, social interactions, or essential resources, individuals of all focal species voluntarily chose to interact with the SEDs, resulting in a considerable amount of time spent with the enrichment items. Furthermore, as we could find no signs that SEDs compromise the welfare of the focal animals, we regard SEDs as a resource efficient possibility to provide novelty as well as opportunities for time occupation and choice. Our data suggests that the individual, not the species, might be the decisive predictor for enrichment interaction with unspecific enrichments as SEDs. This should be investigated further to inform future enrichment concepts for small mammals. We conclude that SEDs may play a vital role in the enrichment of small mammals and can be a good starting point for offering effective behavioral enrichment on a low effort and low-cost basis. Especially in animal houses with many (mixed species) exhibits inhabited by large numbers of individuals, SEDs appear to be an indispensable and valuable tool.

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Supplementary Materials

Results of Statistical Analyses after Exclusion of Data of Individuals with One Observation Unit

Table S1

GLM Selection Analysis with Response Variables 'Enrichment Interaction' and 'Stereotypic Behavior' based on Analysis of Deviance Table, the Corrected Akaike's Information Criterion (AICc), and the (adjusted) McFadden's pseudo-R².

Model	Analysis of Deviance Table					AICc	McFadden's pseudo-R^2	adjusted McFadden's pseudo-R^2
	Resid. Df	Resid. Deviance	df	Deviance	*p*-value			
GLMs with the response variable 'Enrichment interaction'								
Null model	458	13163.9				14860.2	.0	-.0001346
SED+sp	447	5821.8	11	7342.1	<.001	7540.7	.4941475	.4925322
SED+sp/ind	420	4489.1	27	1332.7	<.001	6268.8	.5838431	.5785935
SED+ind	420	4489.1	0	.0		6268.8	.5838431	.5785935
SED+age+time+sp/ind	418	4488.9	2	.2	.913	6273.4	.5838554	.5783365
GLMs with the response variable 'Stereotypic behavior'								
Null model	458	14355.2				14655.8	.0	-.0001364
SED+sp	447	8100.2	11	6255.0	<.001	8423.5	.4268523	.4252145
SED+ind	420	3168.2	27	4932.0	<.001	3552.2	.7634217	.7580988
SED+age+time+ind	418	2610.3	2	557.9	<.001	2999.2	.8014921	.7958963

Note. The GLMs are based on a dataset from that individuals with a single observation were excluded. All p-values '< .001' equal $< 2.2e^{-16}$. The best fitting model based on the used values is printed in bold whereas the finally chosen GLM is highlighted in gray. Due to rare observations of stereotypy, concerning GLMs suffer from zero-inflated data (Figure 2). Therefore, despite of the values used for model selection, we chose the lesser complex GLM with the response variable 'stereotypic behavior' to accomplish GLM-based comparisons. The zero-inflated stereotypy data also caused model overfitting in GLMs including fixed effects that could not be executed with the utilised algorithms. Age = age group, (young or adult); EI = names for GLMs with response variable 'enrichment interaction'; ind = individual; SED = simple enrichment devices; sp = species; ST = names for GLMs with response variable 'stereotypic behavior'; time = time of observation (morning or afternoon).

Table S2

Type II Analysis of Variance Tables (ANOVA) for the Best Fitting GLMs for the Response Variables 'Enrichment Interaction' and 'Stereotypic Behavior'

Response Variable ▶	Enrichment Interaction				Stereotypic Behavior			
Predictor Variable ▼	Wald χ2	df	*p*-value		Wald χ2	df	*p*-value	
SED	4469.6	2	< .001	***	3.7	2	.159	ns
Individual	3042.3	36	< .001	***	2732.9	36	< .001	***

Note. The GLMs are based on a dataset from which individuals with a single observation were excluded. The significance code of three asterisks marks a highly significant p-value, 'ns' stands for a non-significant result. All *p*-values '<.001' equal $< 2.2e^{-16}$, adjusted significance level after Bonferroni correction is $\alpha_j = .025$. SED = simple enrichment devices.

Results of statistical analyses after exclusion of data of species with less than two focal individuals

Table S3

Selection analysis with response variables 'enrichment interaction' and 'stereotypic behavior' based on analysis of deviance table, the corrected Akaike's information criterion (AICc), and the (adjusted) McFadden's pseudo-R

Model	Analysis of Deviance Table					AICc	McFadden's pseudo-R^2	adjusted McFadden's pseudo-R^2
	Resid. Df	Resid. Deviance	df	Deviance	*p*-value			
GLMs with the response variable 'Enrichment interaction'								
Null model	429	11610.4				13145.3	.0	-.0001521
SED+sp	421	5331.9	8	3990.5	<.001	6883.3	.4776904	.4763208
SED+sp/ind	394	3991.4	27	1340.5	<.001	5603.1	.5796851	.5742071
SED+ind	394	3991.4	0	0.0		5603.1	.5796851	.5742071
SED+age+time+sp/ind	392	3990.5	2	0.9	.636	5607.	.5797539	.5739715
GLMs with the response variable 'Stereotypic behavior'								
Null model	429	13835.2				14111.5	.0	-.0001417
SED+sp	421	8055.3	8	5779.8	<.001	8348.1	.4096419	.4083662
SED+ind	394	3117.6	27	4937.8	<.001	3470.7	.7596028	.7544999
SED+age+time+ind	392	2571.6	2	545.9	<.001	2929.5	.7982966	.7929102

Note. The GLMs are based on a dataset from that species with < 2 individuals were excluded. All *p*-values '<.001' equal < $2.2e^{-16}$. The best fitting model based on the used values is printed in bold whereas the finally chosen GLM is highlighted in gray. Due to rare observations of stereotypy, concerning GLMs suffer from zero-inflated data (Figure 2). Therefore, despite of the values used for model selection, we chose the lesser complex GLM with the response variable 'stereotypic behavior' to accomplish GLM-based comparisons. The zero-inflated stereotypy data also caused model overfitting in GLMs including fixed effects that could not be executed with the utilised algorithms. Age = age group, (young or adult); EI = names for GLMs with response variable 'enrichment interaction'; ind = individual; SED = simple enrichment devices; sp = species; ST = names for GLMs with response variable 'stereotypic behavior'; time = time of observation (morning or afternoon).

Table S4

Type II analysis of variance tables (ANOVA) for the best fitting GLMs for the response variables 'enrichment interaction' and 'stereotypic behavior'

Response Variable ▶	Enrichment Interaction				Stereotypic Behavior			
Predictor Variable ▼	Wald $\chi 2$	df	*p*-value		Wald $\chi 2$	df	p-value	
SED	4099.1	2	< .001	***	4.6	2	.09843	ns
Individual	2111.1	33	< .001	***	2697.1	33	< .001	***

Note. The GLMs are based on a dataset from which species with < 2 individuals were excluded. The significance code of three asterisks marks a highly significant p-value, 'ns' stands for a non-significant result. All *p*-values '<.001' equal < $2.2e^{-16}$, adjusted significance level after Bonferroni correction is α_j =.025. SED = simple enrichment devices.

Results of statistical analyses after exclusion of data of individuals with one observation unit and data of species with less than two focal individuals

Table S5

GLM selection analysis with the response variables 'enrichment interaction' and 'stereotypic behavior' based on analysis of deviance table, the corrected Akaike's information criterion (AICc), and the (adjusted) McFadden's pseudo-R^2

Model	Analysis of Deviance Table					AICc	McFadden's pseudo-R^2	adjusted McFadden's pseudo-R^2
	Resid. Df	Resid. Deviance	df	Deviance	*p*-value			
GLMs with the response variable 'Enrichment interaction'								
Null model	428	11572.8				13107.7	.0	-.0001526
SED+sp	420	5324.1	8	6248.6	<.001	6875.5	.4767865	.4754130
SED+sp/ind	394	3991.4	26	1332.8	<.001	5600.7	.5784795	.5731383
SED+ind	394	3991.4	0	0.0		5600.7	.5784795	.5731383
SED+age+time+sp/ind	392	3990.0	2	0.9	.636	5604.6	.5785485	.5729021
GLMs with the response variable 'Stereotypy								
Null model	428	13822.2				14098.5	.0	-.0001418
SED+sp	420	8051.0	8	5771.2	<.001	8343.8	.4094034	.4081265
SED+ind	394	3117.6	26	4933.5	<.001	3468.3	.7593815	.7544157
SED+age+time+ind	392	2571.6	2	545.9	<.001	2927.1	.7981109	.7928614

Note. The GLMs are based on a dataset from that individuals with a single observation and species with < 2 individuals were excluded. All *p*-values '<.001' equal < $2.2e^{-16}$. The best fitting model based on the used values is printed in bold whereas the finally chosen GLM is highlighted in gray. Due to rare observations of stereotypy, concerning GLMs suffer from zero-inflated data (Figure 2). Therefore, despite of the values used for model selection, we chose the lesser complex GLM with the response variable 'stereotypic behavior' to accomplish GLM-based comparisons. The zero-inflated stereotypy data also caused model overfitting in GLMs including fixed effects that could not be executed with the utilised algorithms. Age = age group, (young or adult); EI = names for GLMs with response variable 'enrichment interaction'; ind = individual; SED = simple enrichment devices; sp = species; ST = names for GLMs with response variable 'stereotypic behavior'; time = time of observation (morning or afternoon).

Table S6

Type II analysis of variance tables (ANOVA) for the best fitting GLMs for the response variables ‘enrichment interaction’ and ‘stereotypic behavior’

Response Variable ▶	Enrichment Interaction				Stereotypic Behavior			
Predictor Variable ▼	Wald χ2	df	*p*-value		Wald χ2	df	*p*-value	
SED	4099.1	2	< .001	***	4.6	2	.098	ns
Individual	2111.1	32	< .001	***	2697.1	32	< .001	***