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In search of the optimal enrichment program for zoo-housed animals

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Abstract

Zoo-housed animals are regularly exposed to new forms of environmental enrichment to make their lives less predictable. However, providing new enrichment can have unpredictable effects. We evaluated the effectiveness of two enrichment regimes: (1) providing only new enrichments – "Novelty" and (2) only familiar enrichments – "Familiar." In this case study, enrichment efficacy was assessed using activity budget analysis and novel object tests. The subjects were two focal animals: the golden jackal (*Canis aureus*) and the European badger (*Meles meles*). Our results suggest that both assessment methods provided similar conclusions about the animal's welfare. The "Familiar" treatment significantly increased activity and decreased abnormal behavior in the jackal's activity budget, who avoided novel objects in her baseline novel object test. The Novelty treatment resulted in the growth of time the jackal spent in the moat instead of the main enclosure, and an increase in avoidance and abnormal behaviors. In contrast, the badger demonstrated a high intensity of exploratory behavior in the baseline novel object test, and both regimes led to an increase in the activity budget of the badger. We propose that a stable, but complex enrichment can be an effective robust tool to increase animal welfare, but its efficacy depends on the novelty preference of individual animals. A novel object test can be a rapid tool to assess individual animals' novelty preferences, and this information may help to choose optimal enrichment regimes for individual animals.

KEYWORDS

complexity, data collection, European badger, evaluation, golden jackal, novel object test, novelty, welfare

1 | INTRODUCTION

Zoos and aquariums provide animals with environmental enrichment, defined as various techniques to provide animals with behavioral opportunities important to supporting positive welfare and provide animals with opportunities to have control and choice over aspects of their environment (Brando & Buchanan-Smith, 2018; de Azevedo et al., 2007; Maple & Perdue, 2013). Maximizing enrichment novelty is assumed to be more effective given the generally static nature of captive environments (Clubb & Mason, 2007) and generally rapid habituation to enrichment (Canino & Powell, 2010; Carlstead et al., 1991; Gilbert-Norton et al., 2009; Podturkin et al., 2008; Quirke & O'Riordan, 2011; Szokalski et al., 2012). However, sometimes new enrichment may have undesirable effects like increases in abnormal behavior, aggression, or a decrease in exploration (Bauer et al., 2013; Dobberstine & Shepherdson, 1994; Hahn et al., 2000; Hawkins, 2007; Honess & Marin, 2006; Kolter & Zander, 1995). Understanding how the novelty of enrichments may impact animal responses can therefore help animal managers optimize environmental enrichment programs.

Novelty alone is a psychological stressor (Ader, 1970; Hennessy & Foy, 1987; Mason, 1968) and responses to novelty can be shaped by the

conditions an individual animal experienced. Animals have been shown to be more sensitive to stressors when housed in predictable barren and under stimulating environments, as well as in conditions with high levels of unpredictability combined with low opportunity for choice and control (Destrez et al., 2013; Fox & Millam, 2007; Harding et al., 2004; Inglis, 1975; Renner & Rosenzweig, 1987). The manifestation of high sensitivity has been shown in the form of avoidance of the novel object during novel object tests (Destrez et al., 2013; Podturkin & Popov, 2012) or in the elevation of stress hormones (Hennessy, 2013; Muir & Pfister, 1986). In both cases, perceived lack of control as well as few opportunities for choice under suboptimal conditions can increase an individual's sensitivity to stressors (Neprintseva et al., 2006). Therefore, the provision of novel enrichments to an individual that is kept under suboptimal conditions may increase their sensitivity to stressors and it therefore can reduce its welfare.

As animals need a sense of agency to function effectively and have positive welfare (Allard & Bashaw, 2019; Franks & Higgins, 2012), a preliminary evaluation of the sensitivity of an animal to novelty can help avoid negative reactions to enrichment. Sensitivity to novelty can be measured by the intensity of an individual's exploratory behavior during novel object tests (Podturkin & Popov, 2012), where the intensity of exploration increases with decreasing sensitivity of the animal to novelty that reflect the subjective perception of animals of their own environment (optimal or suboptimal condition, Figure 1; Neprintseva et al., 2006).

Effective enrichments should not compromise the welfare of animals receiving them, either due to causing excessive stress or fear

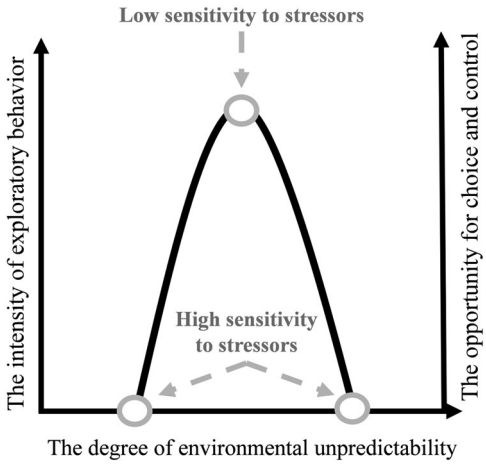

FIGURE 1 The predictive model of exploratory behavior (Modified from the "Stress optimization model" (Neprintseva et al., 2006)). The sensitivity of animals to a stressor can be measured by their intensity of exploratory behavior during novel object tests.
A decrease in avoidance of the object during a novel object test indicates lower sensitivity to stressors (optimal functioning) and that the animal's current environment optimally balances the level of predictability and control. An increase in avoidance of the novel object indicates higher sensitivity to stressor (suboptimal functioning) and that the animal's current environment is not optimally balancing predictability and control (e.g., too predictable or too unpredictable)

responses. But novelty does not always have a negative impact on welfare, as evidence suggests providing appropriate challenges improves animal well-being (Meehan & Mench, 2007) through familiar challenges (Abou-Ismail & Mendl, 2016; Healy & Marples, 2000). Providing familiar challenges to animals can also be an effective method for managing excessive avoidance responses to novelty (Podturkin & Popov, 2012).

Two solitary-housed animals from the order Carnivora, who exhibited stereotypic behavior, were chosen for conducting two similar experiments. Carnivores have been suggested to react more strongly to potential negative effects of captivity (Clubb & Mason, 2007), therefore the manipulation of the level of novelty they experience through enrichment regimes can have a large impact on their welfare.

This pilot study investigates the effectiveness of two enrichment regimes with different novelty levels: (1) only novel enrichments and (2) only familiar enrichments (e.g., types of enrichment used in the previous enrichment treatment).

We expected animals' responses during novel object tests would predict how the animals would respond to enrichment regimes differing in novelty levels. We also expected changes in how animals respond to novel object tests after being exposed to different levels of novelty. Specifically, we expected animals showing high levels of exploratory behavior during initial novel object tests would respond well to the high novelty treatment, showing an increase in overall activity levels, decreases in abnormal behaviors, and changes to how they used their spaces. We predicted animals showing low levels of exploratory behaviors during initial novel object tests would respond better to the familiar only enrichment treatment, and this would be reflected by an increase in overall activity levels, and decreases in abnormal behaviors.

2 | MATERIALS AND METHODS

The study involved two focal animals: the golden jackal (*Canis aureus*) and the European badger (*Meles meles*). The research was conducted in accordance with the guidelines for the treatment of animals in behavioral research and teaching (Buchanan et al., 2012). Experiments with both animals had common elements, but also some differences related to the intensity of data collection and the degree of novelty provided to the animals.

For each animal, we collected time budget data during three experimental phases: baseline, novel enrichments (Novelty), and familiar enrichments (Familiar). After the completion of each phase, the animals received a novel object test with a feeding enrichment. There was a 1-week break with no observations between Novelty and Familiar treatments with the enrichment from the Novelty phase discontinued. The jackal's time budget data was collected for 30 min sessions using instantaneous scan sampling and all occurrence sampling. Since the badger's care staff had limited amount of time for behavioral data collection, the badger was observed with a "multi-point scan" method which is comparable to intensive sampling regimes (Margulis & Westhus, 2008). We wanted to see whether time

budget data collection would lead to similar conclusions about the animal's welfare when compared to the novel object tests.

During the Baseline phase, we collected behavioral data for each animal to analyze their activity budgets when they were fed according to their normal husbandry without the introduction of new enrichment (see below).

During the Novelty treatment, the animals were provided only with new enrichment methods they had not encountered before. The items were smaller than the animals' size in an effort to minimize fear responses and to be distinguishable from large feeding enrichments during novel object tests. The items were placed in random places in the enclosure (Tables 2 and 4). Due to differences in animal management, the jackal received a daily set of four new enrichment items, while the badger was offered only one new enrichment item every third day.

During the Familiar treatment, the animals were exposed simultaneously to all of the enrichments that were mastered at the Novelty phase. Enrichment was considered mastered by the animals if the item was destroyed, moved, or food was extracted. These objects were put in the fixed places in the enclosure. The badger mastered all the provided items during the Novelty treatment, and the jackal only mastered a few. Therefore, during the Familiar treatment, the badger was exposed simultaneously to all 8 enrichments familiar to him from the previous stage, and the jackal was exposed simultaneously to five mastered enrichments.

Enrichments were offered during the routine feeding time, which did not change during the study. All observations were conducted during hours the zoo was open to the public from 10:00 to 17:00, and were carried out in a randomized order throughout an observation day. When using the interval observations, data were recorded directly. Four categories, namely, activity, inactivity, abnormal activity, and out of sight were recorded during this study (Table 1). Additionally, we documented the location of the animals in the exhibit (see below for separate information on each animal) and the average daily temperature. A level of at least 95% agreement between observers (two experienced observers for the jackal behavior and five zookeepers for the badger behavior) was reached.

After the completion of each phase, the animals were offered a novel food-based enrichment item they had not encountered before. The object was obviously larger than the size of the animal and represented a challenge to extract food (Tables 3 and 5). The objects were placed in the open part of the central area in the enclosure once the animals already were in the exhibit (there was no opportunity for the animals to be shifted to an indoor area). The reactions of the animals to the novel object tests were videotaped. The recording was started 1 min before the introduction of the novel object. From the video recordings, a single observer coded the animal's behavior using the Behavioral Observation Research Interactive Software (Friard & Gamba, 2016). We calculated the duration and counted the frequency of each behavior. We recorded three latencies related to an object (first physical contact; approach, e.g., animal approaches within 2 m of the object; extracting the food). We also recorded the duration of interactions with the novel object, normal and stereotypic behaviors, and time spent in shelter or moat (where applicable). At the end of the test, the novel object was removed from the enclosure, and animals were offered a familiar enrichment item.

2.1 | Experiment 1

This study took place between the end of July and the end of September 2016 at Moscow Zoo, Russia. The subject of this study was an adult female golden jackal (*C. aureus*), singly housed in an outdoor exhibit that measured approximately 250 m^2. The exhibit has two zones: Zone 1 (enclosure) that had grasses, wooden shelters, rocks, logs, trees, a spinning feeder with PVC pipes, and Zone 2 (a dry moat). Daily the jackal received food in the two different areas of the enclosure without any additional enrichment. This was termed the Baseline regime for the study.

During the Novelty treatment, over 2 weeks, each day the jackal was exposed simultaneously to four new enrichments from food-based, olfactory, and physical enrichment categories (see Table 2 for all items). Slices of meats, pieces of fruits, quail eggs, and cottage cheese were used to make food-based enrichment.

During the Familiar treatment, for 2 weeks, every day the jackal was exposed simultaneously to the same five items that were mastered at the Novelty phase (Table 2), which were placed on the same spots in the enclosure.

Activity budget data were recorded during in-person focal instantaneous sampling with half-minute inter-scan intervals (Martin & Bateson, 1993). We conducted three 30-min-long observation sessions per day. In total, we collected 48 h of observations including 32 sessions per each experimental phase. We excluded a behavior occurring in less than 1% of all interval observations from further analysis (hunting, drinking, urinating, rolling, digging the ground with hind legs, begging, and out of sight) due to the small sample size. At the same time as instantaneous sampling data collection, we used all occurrence "marking and howling" behaviors to compare the jackal's behavior to observations from a similar study (Gilbert-Norton et al., 2009). All occurrence observations of marking and howling behaviors were added in after the baseline observations had already started and in total, we collected 21 sessions per each phase for this data. The average temperature declined from 25°C to 8°C during the study. The results of a Spearman's rank correlation showed no significant effect of temperature on the jackal behavior, compared to the factor "Enrichment treatment" (see Supplementary 1). Subsequently, the factor "Temperature" was excluded from further analysis.

The novel object tests were recorded for 75 min. New large slotted boxes with double wall measuring 110 × 70 × 70 cm^3 with food inside were used as test objects. The novelty was achieved by changing the orientation of the object (e.g., rotating vertically or horizontally), closing the inner or outer flaps of the boxes, and painted designs on the boxes (Table 3). At the end of the whole experiment, an additional fourth test was carried out, and the object was designed from materials previously unknown to the animal, to avoid the possible effect of habituation on the previous test objects.

TABLE 1 Ethogram used for interval behavioral observations

Behavior category	Behavior	Description	Jackal	Badger
Inactivity	Lying down	Lying down with eyes open or closed	+	+
	Standing	Immobile with all four feet on the ground	+	+
	Sitting	Sitting without performing any other described behavior	+	+
Activity	Behavior directed at enrichment	Pulling, pushing, dragging, chewing enrichment object	+	+
		Digging or pawing at an object; very active with hind legs flexed paws	+	–
		Walking or trotting around with object in mouth	+	+
		Pouncing on and pawing at things	+	–
	Sniffing an enrichment object	Sniffing an enrichment object	+	–
	Inspection (Seeking)	Sniffing the ground, trees, and plants, when not aimed at the acquisition of food or enrichment object	+	–
	Locomotion	Walking, trotting, or running from one place to another	+	+
	Nest-building	Bringing straw and branches into the shelter using paws or in the mouth	–	+
	Feeding	Consuming food (visible jaw movement)	+	–
	Drinking	Drinking water; usually while standing	+	–
	Marking	Urinating (flexing forward and partially lifting a hind leg)	+	–
		Rolling – lying on back and moving from side to side on the ground	+	+
		Digging the ground with hind legs	+	–
	Self-directed (grooming)	Nipping, licking, or scratching its own fur or skin	+	+
	Hunting	Running toward birds – typically trying to catch wild crows	+	–
	Howling	Vocalization ranging from the bark of short duration to a continuous howl	+	–
Abnormal behavior	Pacing	A repetitive movement (with no apparent goal or function) during which the animal repeats the exact movement for greater than three cycles	+	+
	Begging	Animal is sitting or standing in the dry moat directing attention toward visitors (more than 5 s) as they walk past the exhibit.	+	–
	Excessive self-grooming	Extensive nipping its own fur or skin (lasting more than 5 s) with whining	+	–
Out of sight	Shelter	The animal is out of view. The location (shelter 1 or shelter 2[a]) was also recorded	+	+

[a]Both shelters (1 and 2) were only for the badger.

2.2 | Experiment 2

The second study took place from the end of July through to the beginning of October 2018 at Yekaterinburg Zoo, Russia. The subject of this study was an adult male European badger (*M. meles*), singly housed in an outdoor exhibit that measured approximately 19 m^2. The enclosure had grasses, logs, a hanging tire, and a wooden shelter (shelter 1). The majority of the animal's food was offered in a bowl, and the other part was received during the positive reinforcement training sessions. This was termed the Baseline regime for the study.

During the Novelty treatment, every third day over the course of 2 weeks the badger was offered one new food-based enrichment (Table 4). Slices of meats, pieces of fruits, and quail eggs were used to make food-based enrichment.

During the Familiar treatment, over the course of 2 weeks every day the badger was exposed to the same eight items (that were mastered at the Novelty phase) in the same places of the enclosure (Table 4). At the beginning of this phase, an additional wooden shelter (shelter 2), similar to shelter 1, was provided to give the badger even more choice and control over its environment.

The "multi-point scan" method (Margulis & Westhus, 2008) was used by keepers to collect the badger's activity budget data. Keepers were asked to collect data for each phase of observations and were instructed on assessment methods and the ethogram (Table 1). They conducted from 7 to 11 scans per day to record behavior and the location of the animal in the exhibit when they passed the exhibit during their daily routines. The badger's enclosure was divided into several areas: closest to visitors (Zone 1), central (Zone 2), farthest from visitors (Zone 3), shelter 1 (Zone 4), additional shelter (Zone 5) that was situated in the Zone 2. A

TABLE 2 The forms of enrichment used for the jackal during the Novelty and Familiar treatment. Enrichment items were offered in the enclosure (Zone 1)

No.	Enrichment methods	Novelty phase	Familiar phase
1	Food inside burlap sack/craft paper bag/cardboard box (10 × 5 cm^2) hung from a tree	+	+
2	Food inside burlap sack/craft paper bag/cardboard box (10 × 5 cm^2) placed on the floor	+	+
3	Cardboard box 30 × 15 cm^2 with or without food	+	+
4	Chunks of fruits scattered around the enclosure	+	+
5	Food placed inside small Kongs®	+	+
6	Corn cobs	+	–
7	Cow femur	+	–
8	Pumpkin with feed inside	+	–
9	Food placed in a rubber ball (Ø 18 cm) with a hole inside	+	–
10	Food buried at a depth of 5 cm in soil and covered with a pile of dead leaves	+	–
11	Burlap sack with straw	+	–
12	Traffic cone	+	–
13	Chunk of firehose (15 cm)	+	–
14	Essential oils sprayed on empty a cardboard box (10 × 5 cm^2)	+	–
15	Straw bedding from guinea pig enclosure in a cardboard box (10 × 10 cm^2)	+	–
16	Burlap sack with the smell of hoofstock faeces	+	–

Note: Ø – diameter.

TABLE 3 Description of objects for testing the female jackal during the novel object tests

Phase	Novel object
After Baseline (Test 1)	Food was placed in a slotted box with double wall (L110 × W70 × H70 cm^3), where only the inner flaps on the top were open.
After Novelty Treatment (Test 2)	Food was placed in a slotted box with double wall (70 × 70 × 110 cm^3), where only the two outer flaps of the side were open. Nontoxic paint was applied to the front panel (vertical and horizontal stripes).
After Familiar Treatment (Test 3)	Food was placed in a closed cardboard box (30 × 15 × 12 cm^3) that was set inside a slotted box with double wall (70 × 70 × 110 cm^3) where all flaps were folded.
After Familiar Treatment (Test 4)	The food is placed on top of a cardboard tube (L 110 cm, Outer diameter 10 cm), which is placed inside a plastic barrel without a lid (Volume 51 L, H 60.5 cm, Outer Ø 38.2 cm).

Note: L – length; W – width; H – height; Ø – diameter.

total of 224 scans were collected and included in the analysis. The average temperature declined from +27°C to 10°C during the study. The results of a Spearman's rank correlation showed no significant effect of temperature on the badger behavior, compared to the factor "Enrichment treatment" (see Supplementary 2). Subsequently, the factor "Temperature" was excluded from further analysis.

The novel object tests were videotaped for 20 min. Enrichments that were not used during the Novelty and Familiar treatments were used during the tests, and the objects were larger than the animal (Table 5).

2.3 | Data analysis

A Friedman ANOVA was carried out to test if the animals' behavior and use of enclosed space from the activity budget data were influenced by the enrichment regimes. A Wilcoxon signed-rank test with "False Discovery Rate" (FDR) correction (Benjamini & Hochberg, 1995) was performed to determine significant pair-wise relationships. Statistica 6.1 (StatSoft Inc.) and Microsoft Excel 2010 were used for analyses. One day became a unit of analysis. The alpha level for statistical significance was $p < .05$ for all tests. The statistical analysis of the results of the reaction of

No.	Enrichment methods
1	Food hiding under a wooden board (L60 × W50 cm^2).
2	Food placed in a burlap sack or a paper bag and hiding in the gap (5 cm) between two half logs (L 35 cm, Ø 23 cm) joined to each other.
3	Food securely fixed between strips of a fire hose cube (30 × 30 × 30 cm^3).
4	Food hiding in a cardboard box, which was placed in a bigger cardboard box (with panels no more than 50 cm).
5	Food hiding in a burlap sack or craft paper bag with straw inside, which is hung from furniture on a paper rope at the height (20 cm).
6	Food buried at a depth of 10 cm in soil and covered with a heap of logs and branches.
7	Food buried at a depth of 10 cm in soil and covered with bark dust.
8	Food placed in a double-layer craft paper bag.
9	Additional wooden shelter.[a]

Note: L – length; W – width, H – height; Ø – diameter.

[a]Additional shelter was provided only during Familiar treatment.

TABLE 4 The forms of enrichment used for the badger during the Novelty and Familiar treatment. Enrichment items were offered in a central area of the exhibit (Zone 2)

Phase	Novel object
After Baseline (Test 1)	Food was placed in a slotted box with double wall (20 × 35 × 110 cm^3), where all flaps were folded.
After Novelty (Test 2)	Food is placed on top of a cardboard tube (L 110 cm, outer Ø 10 cm), which is placed inside a plastic barrel without a lid (Volume 50 L, H 59 cm, outer Ø 38 cm).
After Familiar (Test 3)	Food was placed on an inner liner of an old car tire (Ø 120 cm, H 22 cm), a cardboard box (20 × 35 × 110 cm^3) wrapped in the chunk of carpet was inserted into the inner rim of the tire.

TABLE 5 Description of objects for testing the male badger during the novel object tests

animals in the novel object tests was not carried out, due to the small size and its high heterogeneity within the tests; only descriptive statistics of the results are presented.

3 | RESULTS

3.1 | Jackal

3.1.1 | Activity budget of the jackal

Enrichment treatment had a significant effect on all behavior categories: activity, inactivity, abnormal behavior, and the jackal's use of space (Figure 2 and Table 6). Abnormal behavior of the jackal significantly increased during the Novelty phase to 24.17% and then significantly decreased to 0.02% on the Familiar days, mainly due to changes in the level of pacing (Table 7). Time spent Inactive decreased between Baseline (75.83%) and both enrichment phases. Between the enrichment phases, the level of inactivity remained at the same level (44.17% Novelty; 48.33%, Familiar). The level of activity did not change between Baseline (12.5%) and Novelty phases (17.5%), but the introduction of the Familiar regime resulted in the significant growth of activity to 39.7%. On Familiar days, the highest values for locomotion, behavior directed toward enrichment, hunting behavior, and feeding were observed (see Supplementary 3).

The introduction of the Novelty regime resulted in the growth of time spent in the Moat from the Baseline value of 54.17% to 91.67%. During the Familiar treatment, the jackal returned to use the enclosure and time spent not in the moat increased to 73.33%.

All occurrence counts showed that enrichment treatments had a significant effect on both documented forms of behavior (Friedman ANOVA, $X^2 = 15.97$, $df = 2$, $p = .0003$; $X^2 = 20.72$, $df = 2$, $p = .00003$, marking and howling, respectively). During the Familiar phase, the jackal had the highest median frequency of howling and marking compared to the previous phases (Table 8).

3.2 | Novel object tests of the jackal

3.2.1 | Exploratory behavior

In the novel object test After Baseline (Test 1) and After Novelty (Test 2), the jackal had no contact with novel objects, the latency to approach the area near the objects was more than 1100 s and she only spent a minute within 2 m of it (out of 75 min of observations). The total number of approaches to the area near the objects was

3 and 5 for the tests After Baseline and After Novelty, correspondingly (Table 9).

The jackal successfully solved the problems of extracting food from novel test objects only after the Familiar phase. The final novel object test following the completion of both treatments was the most successful. After the Familiar period, the latency to approach the object was sharply reduced to 80 s during Test 3 and to 14 s during Test 4.

3.2.2 | Normal activity and abnormal behavior

During the novel object test After the Novelty phase, abnormal activity decreased by three times and normal activity tripled compared with the baseline test. But the frequency of these two forms of behavior was still high (Table 9). During both tests After Familiar treatment, the level of abnormal behavior declined by 59 times compared with test After Baseline and 16 times compared with the test After Novelty. The total time of normal activity reached almost 99% of the duration of the last two tests.

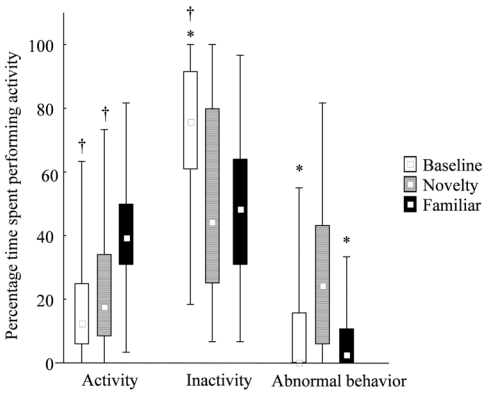

FIGURE 2 Median activity budget data for the jackal under different enrichment treatments (data are presented as the daily median, Q25%, Q75%, min–max). Baseline, Novelty, and Familiar observations. *$p < .05$ versus Novelty; †$p < .05$ versus Familiar (all comparisons were made only within each behavior category)

3.2.3 | Use of enclosed space

During the test After Novelty, the jackal had the lowest time spent in the main part of the enclosure and stayed in the Moat longer than the rest of the other tests (Table 9). After the Familiar treatment, the time spent in the Moat in both tests After Familiar (Tests 3 and 4) was reduced by approximately 18 times compared to the tests After Baseline and Novelty. The time spent in the main part of the enclosure increased by 4.2 and 4.8 times compared to the tests After Baseline and Novelty, respectively.

3.3 | Badger

3.3.1 | Activity budget of the badger

Enrichment treatment had a significant effect on the level of badger's activity, abnormal behavior, and its use of space (Figures 3 and 4; Table 10). Pacing did not change between the Baseline and Novelty phases (11.11%), and then no cases of pacing were recorded during the Familiar regime (Familiar vs. Baseline ($p < .05$), and a tendency for Familiar versus Novelty ($p = .06$). Compared to the Baseline the badger showed significant decreases in the time spent lying down during both enrichment treatments (Table 11). The highest level of activity was during the Novelty phase due to the highest level of locomotion (Table 10). During the Familiar treatment, the activity level was highest due to the amount of behavior directed toward enrichment (37.5%) compared with the other treatments. During the

TABLE 6 Changes in the time budget of the jackal and time spent in different areas of the exhibit (median% (min–max)) under the influence of different enrichment treatments

Type of behavior/ space usage	Baseline	Novelty	Familiar	Friedman ANOVA $N = 32$; $df = 2$ X^2; p-level
Behavior category				
Activity	12.5 (0–63.3)	17.5 (0–73.3)	39.17 (3.33–81.67)	25.59; <.001
Inactivity	75.83 (18.33–100)	44.17 (6.67–100)	48.33 (6.67–96.67)	16.36; <.001
Abnormal behavior	0 (0–55.00)	24.17 (0–81.67)	0.02 (0–33.33)	19.11; <.001
Space usage				
Enclosure	54.17 (0–100)	8.33 (0–68.33)	73.33 (0–100)	23.86; <.001
Dry moat	45.83 (0–100)	91.67 (31.67–100)	29.16 (0–100)	26.38; <.001

Note: P value indicates the result of a Friedman ANOVA. "Baseline": a routine enrichment regime. "Novelty": every day four novel items. "Familiar": every day a complex of five familiar enrichment items.

TABLE 7 The results of a Wilcoxon test (with corrected *p* value) of changes in the time budget of the jackal and time spent in different areas of the exhibit under the influence of different enrichment treatments

Type of behavior/ space usage	Baseline-Novelty			Baseline-Familiar			Novelty-Familiar			Multiple comparisons with corrected *p* (<.05)
	T-statistic	*Z*-score	*p* value	*T*-statistic	*Z*-score	*p* value	*T*-statistic	*Z*-score	*p* value	
Behavior category										
Activity	150	−1.70	.09	28	−4.41	**<.001**	**72.5**	**−3.58**	**<.001**	B vs. F, N vs. F
Inactivity	**65**	**3.72**	**<.001**	**77**	**3.35**	**<.001**	257	0.13	.89	B vs. N, B vs. F
Abnormal behavior	**75.5**	**3.23**	**<.001**	176	0.31	.75	**38.5**	**3.76**	**<.001**	B vs. N, N vs. F
Space usage										
Enclosure	**37.5**	**3.89**	**<.001**	175	−1.43	.15	**24**	**4.40**	**<.001**	B vs. N, N vs. F
Moat	**37**	**−3.91**	**<.001**	148	1.43	.13	**21.5**	**4.44**	**<.001**	B vs. N, N vs. F

Note: Significant multiple comparisons (Wilcoxon signed-rank tests with FDR correction) highlight the difference between phases. Bolded values indicate significant differences. "Baseline": a routine enrichment regime (enrichment item once a week). "Novelty": every day four novel items. "Familiar": every day a complex of five familiar enrichment items.

TABLE 8 Changes in the frequency of marking and howling (median (min–max)) under the influence of different enrichment treatments

Behavior	Situation			Multiple comparisons with corrected *p* (<.05)								
	Baseline	Novelty	Familiar	Baseline-Novelty			Baseline-Familiar			Novelty-Familiar		
	Median (min–max)			*T*-statistic	*Z*-score	*p* value	*T*-statistic	*Z*-score	*p* value	*T*-statistic	*Z*-score	*p* value
Marking	0 (0–4)	0 (0–6)	3 (0–8)	10.5	−1.73	.08	**2**	**−3.53**	**<.01**	**21**	**2.43**	**<.05**
Howling	0 (0–5)	1 (0–10)	4 (0–23)	**4.50**	**−2.53**	**<.05**	**0**	**−3.52**	**<.01**	23.5	−1.82	.07

Note: Significant multiple comparisons (Wilcoxon signed-rank tests with FDR correction) highlight the difference between phases. Bolded values are significant differences.

TABLE 9 Changes in the jackal's reactions to novel objects during the tests under the influence of different enrichment regimes (s; frequency)

Type of behavior	After Baseline (Test 1)	After Novelty (Test 2)	After Familiar	
			(Test 3)	(Test 4)
Latency to approach the novel object (2 m around the object)	1248	1104	80	14
Latency to touch the novel object	4500	4500	172	1584
Latency to extract the food from the novel object	4500	4500	4132	2312
Median duration of interaction with the novel object	0	0	1 (1–10)	1 (1–3)
Total duration of interaction with the novel object	0	0	280; 162	31; 6
Total time spent on the area of the novel object (2 m around the object)	49; 3	43; 5	1170.5; 117	519; 19
Normal activity	1107; 14	3554; 13	4443; 4	4480; 3
Abnormal behavior	3393; 14	946; 15	57; 4	20; 3
Enclosure	1027; 7	889; 4	4305; 3	4410; 4
Moat	3473; 7	3611; 4	195; 2	90; 3

Note: Duration is presented in seconds by total values with frequency per test. The duration of one test was 4500 s.

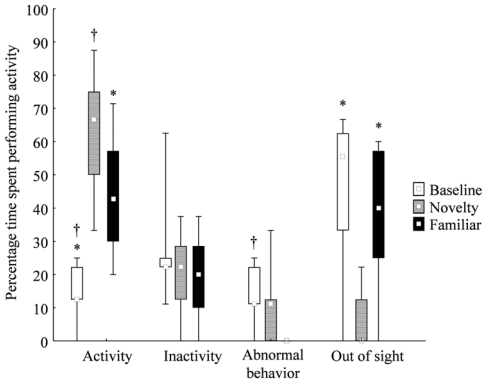

FIGURE 3 Median activity budget data for the badger under different enrichment treatments (data are presented as the daily median, Q25%, Q75%, min–max). Baseline, Novelty, and Familiar observations each have nine sessions. *$p < .05$ versus Novelty; †$p < .05$ versus Familiar (all comparisons were made only within each behavior category); a Friedman ANOVA and followed by Wilcoxon signed-rank tests with FDR correction

Familiar treatment, sitting and nest-building behaviors were observed for the first time (see Supplementary 4).

The introduction of the Novelty regime resulted in the growth of time spent in Zone 2 (where enrichment items were provided) up to 57.14% from 0% (Wilcoxon signed-rank tests with FDR correction: $Z = -2.67$; $p < .05$). During the Familiar treatment, the badger retained the preference for Zone 2 compared with the rest of the exhibit ($Z = -2.52$; $p < .05$, Baseline vs. Familiar) but the absolute amount of time spent in Zone 2 declined significantly (37.5%, $Z = 2.55$; $p < .05$ Novelty vs. Familiar).

The badger significantly reduced the time spent in shelter 1 (Zone 4 or Out of view) during the Novelty regime. However, during the Familiar regime, when an additional shelter was provided (Zone 5), the badger began spending as much time in shelters (Out of view, Zones 4 and 5) as in the Baseline. Although the use of the old shelter (Zone 4) declined with the addition of the new one, the analysis revealed no significant difference between phases (Table 11).

3.4 | Novel object tests of the badger

During the novel object test after the Novelty phase, the badger had the shortest latencies to approach and contact the object, the fastest time of solving the problem of extracting food, the shortest median value of contact with a novel item, and the highest frequency of visits to the area of a new object that were shorter than in other tests (Table 12). But also, the badger had the highest level of abnormal behavior and the lowest median level of normal activity during the test after the Novelty phase compared to other tests.

The median duration of contact with an enrichment object after the Familiar treatment increased by almost 10 times compared to the novel object test after the Novelty treatment, and was 6 times higher than contact with enrichment after Baseline data collection. The time spent in shelters was almost two times what it was after the Familiar treatment than during previous tests. The latencies to approaching the object, to extracting food, and the time spent on the area of the novel object were not different from what was observed during the initial novel object test. During the test after the Familiar phase (Test 3) the median level of normal activity was more than 4.22 times higher than in test After Baseline (Test 1) and more than 8 times higher than the test After Novelty (Test 2). However, the total level of normal activity remained at the level of values in test After Novelty due to the increase in the time spent in the shelter. During the test After Familiar Test 3, the badger did not demonstrate abnormal behavior.

4 | DISCUSSION

In our study, we offered the focal animals two different enrichment treatments (Novelty and Familiar) and observed significant changes in their overall time budget and performance during novel object tests in response to the treatments. We found support for our prediction that animals exhibiting greater sensitivity toward novel objects, as measured by avoidance of the object during novel object tests, changed their response toward novelty after exposure to an enrichment regime providing familiar challenges in familiar locations. Nevertheless, despite the initial difference between the animals' reactions to novelty in the novel object test after Baseline, their response to subsequent tests and their changes in their overall activity budget was shaped by the enrichment treatments. Providing animals with the Familiar treatment resulted in an increase in positive welfare indicators, both in the overall activity budget and in the novel object tests. While the provision of Novelty treatment led to an increase in some negative welfare indicators recorded by the same observation

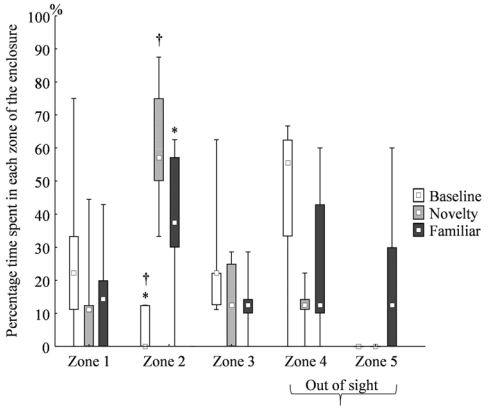

FIGURE 4 Median time spent by the badger in each zone of the enclosure under different enrichment treatments (data are presented as the daily median, Q25%, Q75%, min–max). Baseline, Novelty, and Familiar observations each have nine sessions. *$p < .05$ versus Novelty; †$p < .05$ versus Familiar (all comparisons were made only within each behavior category); a Friedman ANOVA and followed by Wilcoxon signed-rank tests with FDR correction

TABLE 10 Changes in the time budget of the badger and time spent in different areas of the exhibit (median% (minimum–maximum)) under the influence of different enrichment treatments

Type of behavior/ space usage	Baseline	Novelty	Familiar	Friedman ANOVA $N = 32$. $df = 2$ X^2; p-level
Behavior category				
Activity	12.50 (0–25)	66.67 (33.33–87.5)	50.00 (20–71.43)	18.00; <.001
Inactivity	22.22 (11.11–62.50)	22.22 (0–37.50)	20.00 (0–37.5)	1.15; .56
Abnormal behavior	11.11 (0–25)	11.11 (0–33.33)	0	8.31; .02
Out of sight	55.56 (0–66.67)	12.50 (0–22.22)	40 (0–60.00)	7.26; .03
Space usage				
Zone 1	22.22 (0–75.00)	11.11 (0–44.44)	14.29 (0–42.86)	1.11; .57
Zone 2	0 (0–12.5)	57.14 (33.33–87.5)	37.5 (0–62.5)	15.6; <.001
Zone 3	22.22 (11.11–62.50)	12.5 (0–28.57)	12.5 (0–28.57)	0.82; .66
Zone 4	55.55 (0–66.67)	12.5 (0–22.22)	12.5 (0–60)	3.25; .20
Zone 5	–	–	12.5 (0–60)	–

Note: *P* value indicates the result of a Friedman ANOVA. Significant multiple comparisons (Wilcoxon signed-rank tests with FDR correction) highlight the difference between phases. "Baseline": a routine enrichment regime. "Novelty": one new enrichment item every third day. "Familiar": every day a complex of eight familiar enrichment items.

TABLE 11 The results of a Wilcoxon test (with corrected *p* value) of changes in the time budget of the badger under the influence of different enrichment treatments

Type of behavior/ space usage	Baseline-Novelty			Baseline-Familiar			Novelty-Familiar			Multiple comparisons with corrected *p* (<.05)
	T-statistic	*Z*-score	*p* value	*T*-statistic	*Z*-score	*p* value	*T*-statistic	*Z*-score	*p* value	
Behavior category										
Activity	**0**	**−2.67**	**<.001**	**0**	**−2.67**	**.008**	**0**	**2.67**	**<.001**	B vs. N, B vs. F, N vs. F
Inactivity										–
Abnormal behavior	11	0.51	.52	**0**	**2.37**	**<.05**	0	2.02	.06	B vs. F
Out of sight	**4**	**2.19**	**<.05**	15	0.08	.37	**0**	**2.52**	**<.05**	B vs. N, N vs. F

Note: Significant multiple comparisons are highlighted. Significant multiple comparisons (Wilcoxon signed-rank tests with FDR correction) highlight the difference between phases. Bolded values are significant differences. "Baseline": a routine enrichment regime. "Novelty": one new enrichment item every third day. "Familiar": every day a complex of eight familiar enrichment items.

tactics and these negative changes were most noticeable for the jackal, whereas the changes in badger behavior were not so extreme.

It is important for a zoo to understand "how" to optimally deploy enrichment (Popov et al., 2007; Watters, 2009) and understanding an animal's sensitivity to stressors like novelty may facilitate this goal. An abrupt increase in novelty in the environment may lead to negative consequences for animal well-being (Buchanan-Smith, 2011). However, the Novelty treatment resulted in more subtle changes for the badger than for the jackal, which was consistent with the apparent differences in their sensitivity to stressors assessed during the initial novel object test. The jackal initially showed high sensitivity to novelty in the novel object test (avoiding a novel object in the Baseline), and the Novelty treatment resulted in an increase in avoidance and abnormal behaviors. This suggests exclusively novel enrichment was not a "manageable" challenge level for this individual (Meehan & Mench, 2007). This is consistent with studies showing that the enrichment rotation increased neophobia in more fearful individuals than in less ones (Fox & Millam, 2007). Here, we show that providing only familiar enrichment methods allowed both animals, and especially the jackal, to benefit from enrichments and

TABLE 12 Changes in the badger's reactions to novel objects during the tests under the influence of different enrichment regimes (s; frequencies)

Type of behavior	After Baseline Test 1	After Novelty Test 2	After Familiar Test 3
Latency to approach the novel object (2 m around the object)	127	5	117
Latency to touch the novel object	142	15	120
Latency to extract the food from the novel object	182	118	185
Total duration of interaction with the novel object	257.04; 39	113.05; 47	395.47; 14
Median duration of interaction with the novel object	2.28 (0.48–37.92)	1.56 (0.24–19.80)	15.60 (1.32–113.60)
Total time spent on the area of the novel object (2 m around the object)	452.28; 9	242.65; 14	446.77; 7
Normal activity	905.68; 9	641.72; 11	642.67; 5
Abnormal behavior	8.40; 1	249.88; 5	0
Shelter	285.92; 7	308.40; 5	557.33; 5
Enclosure	914.08; 7	891.6; 5	642.67; 5

Note: Duration is presented in seconds by total values with frequency per test. The duration of one test was 1200 s.

significantly improved their willingness to interact with the large novel objects. During the Familiar treatment, both animals exhibited fewer abnormal behaviors overall and showed more exploratory behavior with the novel object during the novel object tests. While during Novelty, both animals, and especially the jackal, exhibited anxiety-like responses (see species-specific behavior discussions below). Manageable challenges and complex conditions provided through familiar enrichments may offer more choice and control to animals, leading to robust improvements in animal welfare, as opposed to overwhelming animals with only novel enrichments.

We found similar changes in jackal behavior during the Familiar treatment as was observed during a study of coyotes (Gilbert-Norton et al., 2009) under the unpredictable regime (see below in Section 4.1). This is consistent with enrichment studies showing differing levels of effectiveness among individual animals (Dobberstine & Shepherdson, 1994; Fox & Millam, 2007; Kolter & Zander, 1995). Novelty preference of an individual may therefore be a more important predictor of behavioral responses to an enrichment regime than taxonomy. We assume that the novelty preference of individual animals could be determined through its sensitivity to stressors (measured by their reaction to novel objects), and this sensitivity will be shaped by enrichment, housing, and husbandry regime the individual experiences. Exploratory behavior can be considered a positive welfare indicator (Watters, Krebs & Pacheco, 2019) and a low exploratory activity may be behavioral indicator of chronic exposure to an aversive stimulation (Carlstead et al., 1993). The jackal was kept for a long time in low-enrichment conditions, so her neophobia is consistent with the studies on sensory deprivation, where animals refuse to use novel items. Reduced exploratory behavior, as mentioned in the introduction, has also been shown in animals after living in unstable unpredictable environments. Thus, the high sensitivity of animals to stressors can be manifested in both under and over-stimulating environments (in our cases, this was after living in low novelty Baseline treatment and then in Novelty treatment conditions). However, providing the animals with a stable but complex environment led to a decrease in their sensitivity to changes and, likely provided them opportunities to respond to environmental changes through applying what had been previously learned. During Familiar treatment, both animals received more enrichment items than during the Novelty phase. Thus, in addition to the fact that the animals were offered manageable challenges on this phase, the absolute amount of enrichment could have an impact on how the animals responded to the treatment as well. Therefore, both parameters could increase the opportunity for choice and control that results in the improvement of animal well-being. We propose that an enrichment regime with only familiar methods is necessary for animals exhibiting high sensitivity to stressors. Whereas the unpredictable regime, which implies the provision of new methods, is more suitable for animals with low sensitivity to stressors like a novelty. Thus, the novelty preference of an individual animal depends on its cumulative welfare, rather than momentary states (Watters & Krebs, 2019), which is formed as a result of the animal's experience of living in an environment with certain characteristics (e.g., novel or familiar enrichment). However, there is a need for further study to confirm this hypothesis.

4.1 | Jackal

The baseline behavior of the jackal was characterized by a high level of inactivity and the presence of abnormal behavior. During the tests after the Baseline phase, the female actively avoided the novel object and spent more time in the dry moat, did not have any contact with the object, and had long and frequent bouts of pacing. We expected to find an increase in the positive indicators of the jackal's well-being only during the Familiar treatment. An

analysis of the activity budget showed that during the Novelty phase, as we predicted, the jackal reduced the time spent in the enclosure (where enrichment items were offered) by 6.5 times compared to the Baseline. The female had decreased inactivity due to increased abnormal activity, exhibited it in the dry moat, and almost did not use new enrichments, only sniffing with low level of without manipulation, and also she started howling. The test results showed similar changes in activity budget data. During the test, the female again actively avoided test object in the dry moat, and still had long bouts of stereotypical behavior.

During the Familiar treatment, as we predicted, the female exhibited positive changes: an increase in normal activity and a decrease in abnormal behavior. The jackal successfully extracted food from all food-based items, increased in time spent locomotion, and spent more time in the main enclosure instead of the moat. Moreover, the female had the highest frequency of howling and vocalization during this phase. This finding is not consistent with the study of coyotes (Gilbert-Norton et al., 2009) in which unpredictable enrichment (randomized by time and location) increased marking and howling, in contrast to the jackal that had the highest frequency of these behaviors during the Familiar treatment, when the objects were fixed in location and predictable in time.

The results of the subsequent tests after Familiar treatment showed the same trends as activity budget data. The jackal successfully extracted food from both large test objects, her abnormal behavior almost completely disappeared, and the female spent in the enclosure almost all the time of the tests.

4.2 | Badger

In the Baseline test, the badger already demonstrated quite a high ability to affect changes in its environment, extracting the food from the novel object in 3 min after the start of the trial. But both assessment methods (activity budget and the novel object test) documented pacing. Despite pacing, we expected to find some positive changes in badger behavior after the Novelty treatment. The analysis of the time budget showed that during the Novelty phase, the level of pacing has not changed, the badger exhibited the highest increase in activity level mainly due to high level of locomotion and increased behavior aimed at enrichment. He also spent more time in the central area of the exhibit where the enrichments were provided, and therefore decreased the time spent in shelters. An active animal in the enclosure increases the level of interest for visitors, but such activity can also reflect a certain level of anxiety in the animal. It is known that in nature a wild badger is spent about 40% of daytime underground (Do Linh San et al., 2010), and the fact that during the Novelty phase the male began to spend only 12% of time in the shelter is rather a negative indicator.

Subsequent novel object tests showed some subtle changes in the animal's behavior. The badger almost immediately approached the large test objects and quickly extracted food. But at the same time, short frequent contacts with the test object and approaches to the area of the object, the frequent bouts of stereotypical behavior can be interpreted as reducing of ability to affect changes in its environment. These findings are consistent with our previous study where the gerbils also had short and frequent contacts with the test object under high uncertainty husbandry conditions (Podturkin & Popov, 2012). Thus, the test reflects a certain ambivalence of the animal's behavior, and its results are concordant with the results of monitoring the activity budget.

The Familiar treatment led to more significant positive changes, both in the activity budget and in the badger's behavior in the test: more natural way of space usage (60% and 40%, enclosure and shelters, respectively), demonstration of new forms of behavior (sitting and building a nest), increase in behavior directed at enrichment, absence of pacing, more persistent and prolonged manipulations with the novel object.

4.3 | Conclusions

In our study, we assessed the ability of two animals to respond to change in their environment using the novel object test and predicted their response to two alternative enrichment treatments. Novelty object tests showed concordant information about changes in animal behavior with the prolonged animal activity budgets, collected in two different ways. Thus, we believe that novelty tests can be a rapid proactive tool for assessing the effectiveness of enrichment that provides useful information for predicting an animal's response to enrichment. We suppose this approach can help to choose the optimal enrichment program, focusing on the novelty preference of individual animals.

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CONFLICT OF INTERESTS

The author declares that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

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

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REFERENCES

Abou-Ismail, U. A., & Mendl, M. T. (2016). The effects of enrichment novelty versus complexity in cages of group-housed rats (*Rattus norvegicus*). *Applied Animal Behaviour Science*, *180*, 130–139. https://doi.org/10.1016/j.applanim.2016.04.014

Ader, R. (1970). The effects of early experience on the adrenocortical response to different magnitudes of stimulation. *Physiology and Behavior*, *5*(8), 837–839. https://doi.org/10.1016/0031-9384(70)90168-X

Allard, S., & Bashaw, M. (2019). Empowering zoo animals, *Scientific foundations of zoos and aquariums* (pp. 241–273). Amsterdam University Press.

Bauer, E., Babitz, M., Boedeker, N., & Hellmuth, H. (2013). Approaches to understanding and managing pacing in sloth bears in a zoological setting. *International Journal of Comparative Psychology*, *26*(1), 53–74.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, *57*(1), 289–300.

Brando, S., & Buchanan-Smith, H. M. (2018). The 24/7 approach to promoting optimal welfare for captive wild animals. *Behavioural Processes*, *156*, 83–95. https://doi.org/10.1016/j.beproc.2017.09.010

Buchanan, K., Burt de Perera, T., Carere, C., Carter, T., Hailey, A., Hubrecht, R., & Peron, F. (2012). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour*, *83*(1), 301–309. https://doi.org/10.1016/j.anbehav.2011.10.031

Buchanan-Smith, H. M. (2011). Environmental enrichment for primates in laboratories. *Advances in Science and Research*, *5*(1), 41–56. https://doi.org/10.5194/asr-5-41-2010

Canino, W., & Powell, D. (2010). Formal behavioral evaluation of enrichment programs on a zookeeper's schedule: A case study with a polar bear (*Ursus maritimus*) at the Bronx Zoo. *Zoo Biology*, *29*(4), 503–508. https://doi.org/10.1002/zoo.20247

Carlstead, K., Brown, J. L., & Seidensticker, J. (1993). Behavioral and adrenocortical responses to environmental changes in leopard cats (*Felis bengalensis*). *Zoo Biology*, *12*(4), 321–331.

Carlstead, K., Seidensticker, J., & Baldwin, R. (1991). Environmental enrichment for zoo bears. *Zoo Biology*, *10*(1), 3–16. https://doi.org/10.1002/zoo.1430100103

Clubb, R., & Mason, G. J. (2007). Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. *Applied Animal Behaviour Science*, *102*(3–4), 303–328. https://doi.org/10.1016/j.applanim.2006.05.033

de Azevedo, C. S., Cipreste, C. F., & Young, R. J. (2007). Environmental enrichment: A GAP analysis. *Applied Animal Behaviour Science*, *102*(3–4), 329–343. https://doi.org/10.1016/j.applanim.2006.05.034

Destrez, A., Deiss, V., Leterrier, C., Boivin, X., & Boissy, A. (2013). Long-term exposure to unpredictable and uncontrollable aversive events alters fearfulness in sheep. *Animal*, *7*(3), 476–484. https://doi.org/10.1017/S1751731112001796

Do Linh San, E., Ferrari, N., & Weber, J.-M. (2010). Circadian activity patterns and nocturnal resting sites of Eurasian badgers (*Meles meles* L.) in a rural area of western Switzerland. *Revue Suisse de Zoologie*, *117*(1), 111–119.

Dobberstine, J., & Shepherdson, D. (1994). Food-scattering enrichment for zoo bears: Does it really work. *Shape of Enrichment*, *3*, 9–10.

Fox, R. A., & Millam, J. R. (2007). Novelty and individual differences influence neophobia in orange-winged Amazon parrots (*Amazona amazonica*). *Applied Animal Behaviour Science*, *104*(1–2), 107–115. https://doi.org/10.1016/j.applanim.2006.04.033

Franks, B., & Higgins, E. T. (2012). Effectiveness in humans and other animals: A common basis for well-being and welfare, *Advances in experimental social psychology* (Vol. 46, pp. 285–346). Elsevier.

Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Gilbert-Norton, L. B., Leaver, L. A., & Shivik, J. A. (2009). The effect of randomly altering the time and location of feeding on the behaviour of captive coyotes (*Canis latrans*). *Applied Animal Behaviour Science*, *120*(3–4), 179–185. https://doi.org/10.1016/j.applanim.2009.06.007

Hahn, N. E., Lau, D., Eckert, K., & Markowitz, H. (2000). Environmental enrichment-related injury in a macaque (*Macaca fascicularis*): Intestinal linear foreign body. *Comparative Medicine*, *50*(5), 556–558.

Harding, E. J., Paul, E. S., & Mendl, M. (2004). Cognitive bias and affective state. *Nature*, *427*(6972), 312. https://doi.org/10.1038/427312a

Hawkins, M. (2007). *Let's rearrange the furniture: The enrichment effects of moving or replacing exhibit furniture*. Paper presented at the Eighth International Conference on Environmental enrichment, Vienna, Austria, August 5–10, 2007.

Healy, E., & Marples, N. (2000). *The effect of enclosure complexity on activity levels and stereotypic behaviour of three species of the genus Panthera at Dublin Zoo*. Paper presented at the Second Annual Symposium on Zoo Research, Paignton Zoo Environmental Park, Paignton, Devon, UK, July 6–7, 2000.

Hennessy, M. B. (2013). Using hypothalamic–pituitary–adrenal measures for assessing and reducing the stress of dogs in shelters: A review. *Applied Animal Behaviour Science*, *149*(1–4), 1–12.

Hennessy, M. B., & Foy, T. (1987). Nonedible material elicits chewing and reduces the plasma corticosterone response during novelty exposure in mice. *Behavioral Neuroscience*, *101*(2), 237–245. https://doi.org/10.1037/0735-7044.101.2.237

Honess, P. E., & Marin, C. M. (2006). Enrichment and aggression in primates. *Neuroscience & Biobehavioral Reviews*, *30*(3), 413–436. https://doi.org/10.1016/j.neubiorev.2005.05.002

Inglis, I. (1975). Enriched sensory experience in adulthood increases subsequent exploratory behaviour in the rat. *Animal Behaviour*, *23*, 932–940.

Kolter, L., & Zander, R. (1995). *Potential and limitations of environmental enrichment in managing behavioural problems of polar bears*. Paper presented at the Second International Conference on Environmental Enrichment, Copenhagen Zoo, Frederiksberg Denmark, August 21–25, 1995.

Maple, T. L., & Perdue, B. M. (2013). Environmental enrichment, *Zoo animal welfare* (Vol. 14, pp. 95–117). Springer.

Margulis, S. W., & Westhus, E. J. (2008). Evaluation of different observational sampling regimes for use in zoological parks. *Applied Animal Behaviour Science*, *110*(3–4), 363–376.

Martin, P., & Bateson, P. (1993). *Measuring behaviour: An introductory guide* (2nd ed.). Cambridge University Press

Mason, J. W. (1968). A review of psychoendocrine research on the pituitary-adrenal cortical system. *Psychosomatic Medicine*, *30*(5 Suppl), 576–607.

Meehan, C. L., & Mench, J. A. (2007). The challenge of challenge: Can problem solving opportunities enhance animal welfare? *Applied Animal Behaviour Science*, *102*(3–4), 246–261. https://doi.org/10.1016/j.applanim.2006.05.031

Muir, J. L., & Pfister, H. P. (1986). Corticosterone and prolactin responses to predictable and unpredictable novelty stress in rats. *Physiology and Behavior*, *37*(2), 285–288. https://doi.org/10.1016/0031-9384(86)90234-9

Neprintseva, E., Popov, S., Ilchenko, O., & Voschanova, I. (2006). Theoretical bases of environmental enrichment as applied to keeper-animal interactions, *Animals, zoos & conservation* (pp. 151–158). Zoological Garden in Poznan.

Podturkin, A., & Popov, S. (2012). Influence of laboratory environment characteristics on exploratory behavior of midday gerbils (*Meriones meridianus*). *Zoologicheskii Zhurnal*, *91*(2), 202–207.

Podturkin, A., Popov, S., & Neprintceva, E. (2008). Environment enrichment for two cheetahs in Moscow Zoo. *Scientific Research in Zoological Parks*, *24*, 45–52.

Popov, S., Iltchenko, O., & Neprintseva, E. (2007). *Unpredictability, controllability and optimal arousal stimulation level as applied to zoo environment enrichment theory and practice*. Paper presented at the Eighth International Conference on Environmental Enrichment, Vienna, Austria, August 5–10, 2007.

Quirke, T., & O'Riordan, R. M. (2011). The effect of a randomised enrichment treatment schedule on the behaviour of cheetahs (*Acinonyx jubatus*). *Applied Animal Behaviour Science*, *135*(1–2), 103–109. https://doi.org/10.1016/j.applanim.2011.10.006

Renner, M. J., & Rosenzweig, M. R. (1987). *Enriched and impoverished environments: Effects on brain and behavior*. Springer

Szokalski, M. S., Litchfield, C. A., & Foster, W. K. (2012). Enrichment for captive tigers (*Panthera tigris*): Current knowledge and future directions. *Applied Animal Behaviour Science*, *139*(1–2), 1–9. https://doi.org/10.1016/j.applanim.2012.02.021

Watters, J. V. (2009). Toward a predictive theory for environmental enrichment. *Zoo Biology*, *28*(6), 609–622. https://doi.org/10.1002/zoo.20284

Watters, J. V., & Krebs, B. L. (2019). Assessing and enhancing the welfare of animals with equivocal and reliable cues. *Animals*, *9*(9):680. https://doi.org/10.3390/ani9090680

Watters, J. V., Krebs, B. L., & Pacheco, E. (2019). Measuring welfare through behavioral observation and adjusting it with dynamic environments. In A. Kaufman, M. Bashaw, & T. Maples (Eds.), *Scientific foundations of zoos and aquariums: Their roles in conservation and research*, (212–240). Cambridge University Press. https://doi.org/10.1017/9781108183147.009.

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