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# Battle of the enrichments: comparing the impact of nutritional and sensory enrichment on the behaviour of captive lowland tapirs *Tapirus terrestris*

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**Abstract**

Environmental enrichment is used to improve the welfare of captive animals by providing increased environmental variety, the provision of choice, and the opportunity to develop competency. The efficacy of a range of environmental enrichment should be measured on a species-by-species basis to encourage species-specific behaviours and to reduce abnormal behaviours. This study aimed to identify whether different types of enrichment affected feeding, locomotive or resting behaviours in two (1.1) captive lowland tapir *Tapirus terrestris* housed at Dartmoor Zoo in the hour after enrichment was provided. A baseline period occurred in which no enrichment was given in the morning. The experimental period followed, in which five nutritional enrichments and four forms of sensory enrichment items were provided, randomly alongside the tapirs' morning feed over a period of three months. Behavioural observations were collected at thirty second intervals during the hour immediately after provision. Generalised Linear Mixed Models found that nutritional enrichment significantly increased feeding behaviour, and this was the case for all five enrichment items, compared with baseline observations. Locomotion, resting and other behaviours were not significantly different compared with baseline observations. Post-hoc comparisons between enrichments revealed significant behavioural differences between enrichment categories. The results indicate that a wide range of enrichment, such as food-based cognitive enrichment and biologically relevant olfactory enrichment, should be used and evaluated in tapir husbandry plans.

## Introduction

### *The study of enrichment*

Enrichment can contribute to animal welfare by providing opportunities for positive subjective experiences via the Domains, as stated in The 2020 Five Domains Model (Mellor et al. 2020). The Five Domains Model is a framework which includes consideration of nutrition, physical environment, health, and behavioural interactions as contributors to the mental state and wellbeing of animals (Mellor et al. 2020). Enrichment can increase nutritional variety (Domain 1) in an animals' diet and provide access to a wider range of the nutritional conditions for which the species evolved. For example, inclusion of bamboo enrichment into the diet of captive Asian elephants *Elephas maximus* increased the amount of time spent foraging and manipulating food items compared to hay feeds (Tscuchiya et al. 2023). The complexity of an animal's physical environment (Domain 2) can also be influenced by enrichment, such by as offering different types and heights of foliage and shelters for callitrichid species (Sha et al. 2016), and thus provide opportunities for various forms of comfort and enjoyable experiences (Mellor et al. 2020). Enrichment can also contribute to an animals' health (Domain 3) by encouraging movement and reducing stress; for example, supplying whole bones as enrichment elicited higher rates of non-stereotypical activity in African lions *Panthera leo* (Bashaw et al. 2002). Positive behavioural interactions (Domain 4) can also be promoted using enrichment (such as the use of public feeding interactions to elicit an increase in social activity performed by African elephants *Loxodonta africana* (Fernandez et al. 2021)) and provide opportunities for the conscious decision-making processes and cognitive agency that animals use in the wild (Coe 2017). As such, Domains 1 to 4 all contribute to the mental wellbeing of animals (Domain 5) (Mellor et al. 2020). Enrichment, when used appropriately in welfare-relevant contexts, may therefore be used to provide the positive subjective experiences needed to improve animals' mental states and wellbeing (Brando et al. 2023).

Previous research has highlighted the importance of accurate enrichment evaluation, particularly on a species-by-species basis (Hoy et al. 2010). Behaviour has been used as a successful metric across many different species through measuring species specific behaviours (Huskisson 2020) and increasing the presence or duration of specific behaviours can be used as a goal for enrichment provision. For example, goats *Capra hircus* climb while foraging, so should be provided with multi-level feeding opportunities (Zobel and Nawroth 2020), whereas pigs *Sus scrofa domesticus* root in substrate, so prefer food in soft ground materials (Mkwanazi et al. 2019). Valuable research assesses a range of enrichment for a single species, and reports both successes and failures to improve husbandry practises (Mason et al. 2006; Yeates et al. 2008). However, strategising enrichment programmes and measuring their impact has proven problematic historically (Swaisgood and Shepherdson 2008); studies in zoos commonly use multiple enrichments at once, making analysis of individual methods difficult (de Azevedo et al. 2007; Swaisgood et al. 2005). Furthermore, published research tends to centre on primates or carnivores (de Azevedo et al. 2007; Rose and Robert 2013). As such, environmental enrichment research should be extended to underrepresented captive species to ensure that individual enrichment practices are promoting their welfare effectively.

### *Enriching lowland tapirs*

Tapirs represent a group for which enrichment assessment is limited (Dutra and Young 2015). Studies have anecdotally suggested that browse enrichment increases activity period length and frequency of swimming in Malayan tapir *Tapirus indicus*, but data are lacking (Rose et al. 2006; Rose and Roffe 2008). In response, a review of occupational enrichment (items or practices which promote cognitive stimulation and/or physical interactions, Laule 2002); nutritional enrichment (involving the presentation of novel food types, or encouragement of specific, natural feeding behaviours, Ghavamian et al. 2022; Klieman et al. 2010); and sensory enrichment (providing increased opportunity for visual, olfactory, auditory or tactile interactions Brando et al. 2023; Martínez-Macipe et al. 2023) used in international tapir husbandry programmes was conducted (Rose and Roffe 2012). This study found that while at least 70% of the participating zoos provided enrichment for their tapir, provision of occupational and sensory enrichment was not ubiquitous (Rose and Roffe 2012). Only enrichment which falls under the 'physical' category has been tested quantitatively. For example, the introduction of bamboo bushes and mounds of leaves were found to significantly increase movement and decrease resting in lowland tapir *Tapirus terrestris*, but had no significant impact on foraging, vocalisation, or swimming behaviours (Dutra and Young 2015). Thus, it is important to address the gap in our understanding of how alternative forms of enrichment (such as sensory enrichment and a wider range of nutritional enrichment), may improve the wellbeing of tapirs (Rose and Roffe 2012).

The lowland tapir is one of four extant, monophyletic species of tapir (including Malayan tapir, mountain tapir *T. pinchaque*, and Baird's tapir *T. bairdii*, Ferrero and Noriega 2007). Tapirs are herbivorous, neotropical browsers, distributed across 11 South American countries (Medici 2011) and occupying a range of habitats from swamp forests to savannahs (de Thoisy et al. 2010). Lowland tapirs are mostly crepuscular and nocturnal (Gomez et al. 2005; Oliveira-Santos et al. 2009), therefore locating tapirs in situ can be difficult, so methodologies for behavioural studies are still being trialled and standardised (Zayonc and Coomes 2021). Captive tapirs are therefore studied more frequently, and research into body condition and diet (Clauss et al. 2009), infection diagnosis (Marcordes et al. 2020) and genetics (da Silva et al. 2010) has been conducted. In this case, we are assessing the impact of different enrichment items on two captive tapirs housed at Dartmoor Zoo.

This study aimed to implement various environmental enrichment, including some that have previously been reported as being used in tapir husbandry, from nutritional and sensory categories (Gilmore 2007; Rose et al. 2006; Rose and Roffe 2012). Enrichment was provided simultaneously to the usual morning feed due to previous research finding a spike in enrichment engagement before 10:00am (Dutra and Young 2015), which is up to 4.5 hours after sunrise. Target behaviours, such as those used to study tapir by Arumugam et al. (2020) including resting, locomotion and ingestion categories, were used to assess enrichment efficacy. As browsers who feed little and often (AZA Tapir Tag 2013), it was hypothesised that nutritional enrichment involving novel food presentation would increase time spent feeding. Additionally, tapirs select home ranges based on provisions such as salt licks, latrines (Montenegro 1998) and access to water sources (Gilmore 2007), and will travel large distances to utilise these resources (Noss et al. 2003; Herrera et al. 1999). As such, it was hypothesised that sensory enrichment (i.e. promoting tactile or olfactory interactions, such as scrub brushes or perfume) would be most effective at increasing locomotive behaviour, and decreasing resting behaviour.

## Materials and methods

### *Study animals and site*

The study was conducted at Dartmoor Zoological Society in southern England (50.407°N 3.997°W) and involved two (n=2) lowland tapirs: a female (Fortuana, 15 yrs), and her son (Rofilho, six yrs). Fortuana was brought to the zoo 12 years ago and subsequently birthed four offspring, the last of which was Rofilho, who has lived at the zoo since birth.

The individuals were housed together in a large paddock (~9063m$^2$) comprised of two fields (~1,200m$^2$ and ~7575m$^2$ respectively) and a partitioned yard (~288m$^2$) containing a heated indoor habitat (~18m$^2$). Two pools, three shelters, and various landscape features such as banks, hills, and trees were present in the fields. A metal trough for food and a tree were located in the yard. The area was surrounded and segregated by wooden and wired fences, with an external road along the western boundary. The road was used for all vehicles and foot traffic entering and exiting the zoo, including both public and staff access. The paddock also housed seven capybaras *Hydrochoerus hydrochaeris*; four Patagonian mara *Dolichotis patagonum*; five greater rhea *Rhea americana*; and five runner ducks (*Anas platyrhynchos domesticus*. Wild mallards *Anas platyrhynchos* and Canadian geese *Branta canadensis* also accessed the paddock during the study period.

The tapirs were fed daily between 0900 and 1000, approximately 1-2 hours after sunrise, with 1400 g Charnwood Browser Maintenance Pellet, 250 g Alpha A, 1 tsp garlic powder, 10ml Equivite Original Supplement, ¼ cup (approximately 60mls) of cod liver oil. Their second feed was given between 1500 and 1600 with


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2 kg root veg, 1.5kg salad veg, 2.5 kg other veg, and 1.5kg leafy veg provided for both animals. Water and natural browse in the hedgerows were available ad libitum throughout the day.

***Preliminary observation***

A preliminary observation period of ten hours (comprising of three sessions between 0900-1000, and seven one hour sessions between 1000-1600) occurred to determine the behavioural repertoire of the study animals between 1 September 2021 and 14 September 2021. Observations were conducted in person from the western road, from which all external areas could be viewed. These preliminary observations alongside a review of genus *Tapirus* and hoofstock (reindeer *Rangifer tarandus*) ethograms in the literature (Arumugam et al. 2020; Gilmore 2007; Kakol 2021) resulted in the identification of seven categories of behaviour. These were: resting, locomotion, feeding, social, 'other', elimination, sexual and agonistic (see Table 1). Two further adjustments were made before the production of a final ethogram, due to 1) no sexual or agonistic behaviour being observed, leading to the removal of these categories, and 2) to account for times when animals were not visible when inside one of the shelters, recorded as 'out of sight'.

***Baseline data collection***

Seventeen baseline observations were conducted between 15 September 2021 and 8 October 2021, on weekdays. Observations were conducted for an hour after the tapirs' morning feed (fed between 0900 and 1000) from the point at which the last tapir stopped feeding. Scan sampling was used to record the behaviour of each tapir every 30 seconds. This resulted in 17 hours of baseline data collection per animal. The ambient temperature reported by The Met Office was recorded at the beginning of each observation. As the tapirs are on the only route into the zoo, all visitors must walk past them; therefore, the number of visitors who entered the zoo between 1000 and 1100 were subsequently collected and used as a measure of visitor numbers during the observation period.

***Experimental data collection***

Nine different enrichment items were devised using tapir husbandry guidelines (AZA Tapir TAG 2013). The enrichment items provided were either completely novel to the study animals or had not been used within a year of the beginning of the study. Five were nutritional based enrichment and four were sensory enrichment (see Table 2). Each enrichment was implemented on five different days between 11 October 2021 to 13 Jan 2022 for 24 hours. The order of implementation was randomised to reduce habituation. Observations began immediately after the last tapir had finished eating the morning feed from the trough and lasted one hour to produce five hours of data collection per individual per enrichment. Ambient temperature and the number of visitors at the zoo during each observation was recorded using the same methods as the baseline data collection.

**Table 1.** Ethogram for Brazilian tapir; adapted from a reindeer ethogram (Kakol 2021), and two tapir ethograms (Arumugam 2020; Gilmore 2007).

| Behaviour category | Behaviour | Description |
|---|---|---|
| Resting | Standing | Still on all fours. |
| | Sitting | Weight on posterior centrally or on the side with front legs extended to the ground. |
| | Lying down | Lying on front with legs folded beneath the body, extended outwards; lying on side with legs beneath the body or extended outwards. |
| Locomotion | Running | Galloping/trotting from one location to another. |
| | Walking | Walking from one location to another. |
| Feeding | Foraging | Looking for or eating natural vegetation in the habitat; looking for or eating food presented with/as enrichment. |
| | Eating/drinking | Consumption of food from trough and/or consumption of water from ponds/streams. |
| Social | Vocalisation | Calling to conspecifics via noises produced in the oral/sinus cavity. |
| | Physical interaction – intraspecific | Sniffing, rubbing against, playing with one another. |
| | Physical interaction – interspecific | Sniffing, rubbing against, or playing with individuals of another species, including keepers. |
| | Following | Locomotion within 1.5 m behind one another, or travelling in the same direction parallel to one another. |
| Other | Water | Playing in/with water; swimming. |
| | Scratching | Rubbing against physical features of habitat |
| | Investigative | Sniffing (including flehmen response), exploring or interacting with physical environment/ enrichment without food consumption. |
| Elimination | Defecation | Expulsion of faeces. |
| | Urination | Expulsion of urine. |
| | Spraying | Bursts of urine expelled posteriorly. |
| Out of sight | Out of sight | Not visible to observer, i.e. inside a shelter. |

Table 2. Types and descriptions of enrichment items used in the tapir habitat. The category of enrichments and descriptions, including dimensions ('L' stands for length, 'V' stands for volume).

| Enrichment type | Enrichment name | Enrichment description |
|---|---|---|
| Sensory | | |
| | New substrates | Wood chips from another site in zoo on wooden pallet (100x100 cm) |
| | Wind chime | Wind chime secured to external beam of shelter(L=75 cm) |
| | Perfume | Four sprays of Coco Chanel on three existing structures |
| | Scrub brush | Scrub brush head secured to fence |
| Nutritional | | |
| | Blended vegetables | 500g of mixed vegetables blended and placed in holes of a tube feeder (L=100 cm) |
| | Vegetable washing line | 1.5kg of whole vegetables hung on a horizontal chain (L=200cm approx.) |
| | Frozen vegetables | 500g of whole vegetables frozen in water using a feed bucket (V=10 L) |
| | Vegetables in pool | 500 g of whole vegetables thrown into pool |
| | Puzzle feeder | Spinning, wooden puzzle feeder containing half of morning pellet mix (approx. 825 g) secured to fence (70x70 cm) |

***Data analysis***
All statistical testing and modelling were conducted using R Studio Interface (version 1.2.5019) (R Core Team 2019).

Each day of observations was treated as an experimental unit (Bishop et al. 2013), a method which has been successful in similar research (Finch and Humphries 2022; Sherwen et al. 2015). The count data from baseline and enrichment periods were converted to proportions by dividing the number of observations of each behaviour per day by the total number of observations. Mean proportions for each behaviour across enrichment categories and during the baseline period were calculated and Shapiro-Wilk testing found all variables to be non-parametric. No analysis was conducted on behaviours which accounted for less than 2% of the tapirs' activity budgets, a cut-off point which has been used in similar studies (e.g. Glaeser et al. 2021) and resulted in the exclusion of social and elimination behaviours.

To compare the behavioural repertoire of the tapir in each enrichment condition with that of the baseline, Generalised Linear Mixed Models (GLMMs) were run for all behaviours (foraging, locomotion, resting, out of sight, and 'other') using the 'lme4' package (Bates et al. 2014). GLMMs were selected to account for the non-normal distribution and non-independence of data points (Bateson and Martin 2021) due to data being collected from the same two individuals. To counteract this, 'tapir' was included as a random effect in the models (Bateson and Martin 2021; Van de Pol and Wright 2009). As the response variables were proportions derived from count data, a binomial family and logit function were used (Crawley 2013). Enrichment category, ambient temperature,

**Table 3.** GLMM results stating the effect of enrichment categories on proportion of observations spent performing each behaviour. 'Std. Error' = standard error, 'Pr(>|Z|)' =P values associated with 'z value'. A value of 0.05 was used to determine significance. '*' indicates Pvalues less than 0.05 and therefore signifies a significant difference.

| Behaviour | Enrichment category compared to baseline | Estimate | Std. error | Z value | Pr(>\|z\|) |
|---|---|---|---|---|---|
| Feeding | Nutritional | 2.5864 | 0.5535 | 4.673 | <0.05 |
| | Sensory | 0.3037 | 0.5880 | 0.516 | 0.61 |
| Resting | Nutritional | -0.9872 | 0.5450 | -1.811 | 0.07 |
| | Sensory | -0.4479 | 0.5284 | -0.848 | 0.40 |
| Locomotion | Nutritional | -0.4709 | 0.6552 | -0.719 | 0.47 |
| | Sensory | 0.1288 | 0.6241 | 0.206 | 0.84 |
| Out of sight | Nutritional | -0.5108 | 0.6048 | -0.845 | 0.40 |
| | Sensory | -0.3887 | 0.6257 | -0.621 | 0.53 |
| Other | Nutritional | 0.260 | 1.477 | 0.176 | 0.86 |
| | Sensory | 1.018 | 1.377 | 0.739 | 0.46 |


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**Table 4.** GLMM results showing the impact of enrichment categories on proportion of observations spent feeding compared with the baseline category.

| Enrichment item compared with baseline | Estimate | Std. Error | z value | Pr(>\|z\|) |
|---|---|---|---|---|
| Blended vegetables | 2.3975 | 0.8246 | 2.907 | <0.01 |
| Frozen vegetables | 2.3963 | 0.8245 | 2.906 | <0.01 |
| New substrates | -0.6869 | 1.1629 | -0.591 | 0.55 |
| Perfume | -0.6865 | 1.1628 | -0.59 | 0.55 |
| Puzzle feeder | 3.6229 | 1.0998 | 3.294 | <0.01 |
| Scrub brush | 0.7055 | 0.8247 | 0.856 | 0.39 |
| Vegetables pool | 2.3986 | 0.8248 | 2.908 | <0.01 |
| Vegetables washing line | 2.4376 | 0.8294 | 2.939 | <0.01 |

and visitor numbers during the study period were all included as fixed effects. The least significant explanatory variable was systematically dropped from the models and the models with the lowest AIC value was used for the final results. Models were validated through the creation of QQ and heteroscedasticity plots using the 'LMERConvenienceFunction' package (Tremblay 2020).

Pairwise Wilcoxon rank sum tests were conducted for post-hoc comparisons to determine differences between individual enrichment items on the tapirs' behaviour. Bonferroni corrections were applied to each test (Hawkins 2009) to mitigate the increased chance of type I error due to the high quantity of tests performed (Andrade 2019). A confidence interval of 95% was used when interpreting P values.

## Results

***Baseline vs. enrichment periods***

When nutritional enrichment was provided, the animals spent a significantly higher proportion of time feeding compared to baseline data, whilst sensory enrichment did not influence the proportion of observations spent feeding (Table 3). Resting, locomotion, out of sight and other behaviours were not significantly affected by nutritional or sensory enrichment provision (Table 3). Table 4 shows time spent feeding was significantly higher during all five nutritional enrichments compared with the baseline period.

***Comparison between enrichment types***

The animals spent significantly less time feeding when provided with the sensory enrichment of new substrates and perfume in comparison to when the feed-based enrichment of blended vegetables (P=0.02) and the puzzle feeder (P=0.05) were provided (Figure 1a). Locomotion was performed significantly more when perfume enrichment was given, compared with 3 nutritional enrichments; vegetables in the pool (P=0.04), frozen vegetables (P=0.02) and vegetable kebabs (P=0.38) (Figure 1b). Feeding enrichment of frozen vegetables yielded significantly lower proportions of resting behaviour than the scrub brush (P=0.02) and perfume enrichment (P=0.04) (Figure 1c). There were no significant differences in the proportion of time spent out of sight or performing 'other' behaviours between enrichment items.

## Discussion

The nutritional enrichment provided in this study significantly altered the feeding behaviour of the tapir in comparison to the baseline, a finding which supports the hypothesis that nutritional enrichment would increase the time that the tapirs spent feeding. This result is consistent with literature concerning nutritional enrichment in a range of captive species such as African elephants (Stoinsky et al. 2000), sloth bears *Melursus ursinus* (Veeraselvam et al. 2013) and dogs *Canis lupus familiaris* (Schipper et al. 2008). In addition, nutritional enrichments blended vegetables and puzzle feeder promoted a higher proportion of time feeding compared with new substrates and perfume respectively, though for most enrichments there was no difference in feeding time. This may be because the tapirs' motivation to feed was lower during enrichment provision as they were fed prior to enrichment installation. Another explanation is that natural browse, and therefore opportunities for foraging, were available around the tapirs' habitat during all conditions. Although the importance of enrichment should not be underestimated, this finding evidences the importance of suitable habitats with ample browsing opportunities in contributing to ungulate wellbeing (Fábregas et al. 2012; Hatt et al. 2005).

It was hypothesised that sensory enrichment would increase locomotion and decrease resting, which is not supported by our results when comparing to baseline behaviour, which is consistent with research on Rothschild giraffe (Clark and Miller 2015) and Icelandic reindeer (Kakol 2021). This may be because the scents, sounds, and textures used were not biologically relevant (i.e. not physiologically meaningful to the tapir) and therefore did not stimulate any species-specific behaviours (Wells 2009). Indeed, a study in which tapirs were allowed to rotate enclosures with predatory species - which produced biologically relevant olfactory enrichment through scent marking – found that the tapir displayed more natural territorial behaviour than before they were provided with opportunity to do so (White et al. 2003). Visual, olfactory and auditory cues are commonly used for inter-and intra-species communication in mammals (Hurst et al. 2008). As the tapirs are housed in a mixed species habitat, they are presented with biologically relevant sensory stimulation each day which likely increased the environmental complexity of their habitat (Veasey and Hammer 2010). Biologically relevant enrichment has been shown to increase activity in captive species, such as exploration in cats *Felis catus* exposed to prey scents (Machado and Genaro 2014) or feeding bouts in horses *Equus ferus caballus* exposed to predator scents (Christensen and Rundgren 2008). Therefore, the tapir may have had ample opportunities to display behavioural diversity due to sensory stimulation which limited the impact of sensory enrichment. Further research assessing the effect of sensory enrichment on the behaviour of tapirs housed as a single species, or within differing enclosures would be beneficial.

The use of perfume as sensory enrichment elicited significantly more locomotion than three forms of feeding enrichment (frozen vegetables, vegetables in the pool and vegetable kebab), partially supporting our hypothesis that sensory enrichment would increase locomotion. Perfume was the only form of enrichment which was provided in multiple regions of the habitat (to prevent other species in the habitat consuming other enrichment items). Whilst we did not assess habitat usage in this study, the tapirs may have been using more of their enclosure as they moved between areas where perfume had been sprayed. This has been seen in both Rothschild giraffe (Clark and Miller 2015) and black-footed cats *Felis nigripes* (Wells and Egli 2004) whereby animals utilised a greater proportion of habitat space in response to novel scents. It stands to reason that more locomotion would be initiated during sensory enrichment than by feeding enrichment, which the tapirs could interact with while stationary. For frozen vegetable enrichment, the lower proportion of time locomoting was seen alongside in lower proportions of resting behaviour compared to the perfume enrichment and scrub brush conditions. This is consistent with research on Icelandic reindeer, who interacted most with enrichment involving novel food presentation, therefore resting less (Kakol 2021). Frozen vegetables did not significantly alter resting compared to the baseline however, and

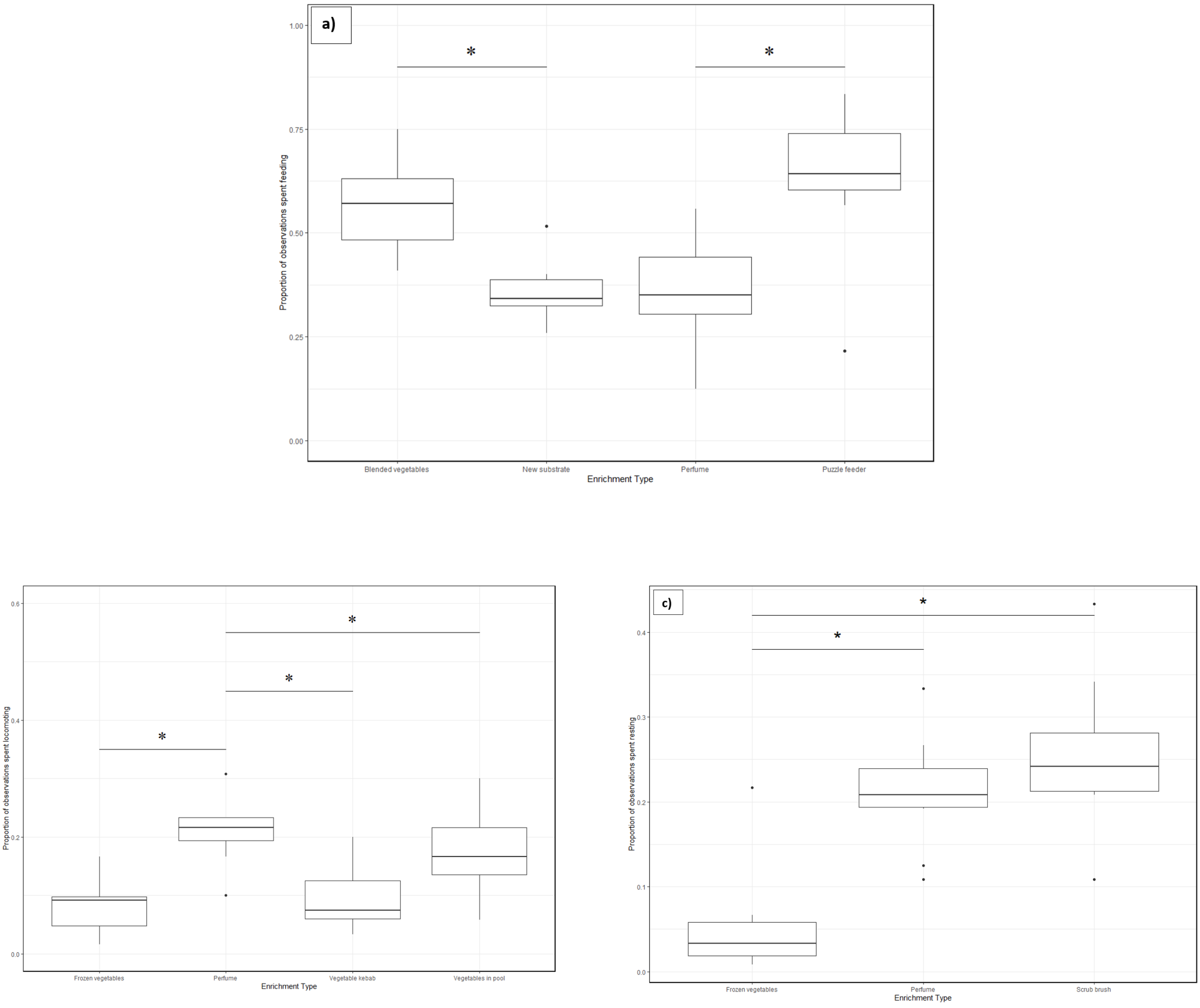


**Figure 1.** a) Boxplots representing proportions of observations the tapirs spent feeding while exposed to different enrichments. b) Boxplots representing proportions of observations the tapirs spent locomoting while exposed to different enrichments. c) Boxplots representing proportions of observations the tapirs spent resting while exposed to different enrichments. * indicates a significant difference.

this highlights the importance of reviewing individual enrichment items. Further research using enrichment dispersed over a larger area of tapirs' habitats would produce a useful comparison for the findings presented in this study.

Feeding and resting behaviours were exhibited most during the experimental period. This contrasts pre-existing tapir activity budgets, which cited resting (~60% of activity in one study, Gilmore 2007; and ~70% in another, Kinahan 2002) and investigative behaviour (18.5% in Gilmore 2007) as the greatest proportions of activity. However, the activity budgets produced by this study represent one hour of the tapirs' diurnal activity directly after feeding, while others used 24-hour observations of behaviour (Gilmore 2007; Mahler 1984), which is likely the cause of these differences. Captive tapirs are most active in the early morning and mid-afternoon (Kinahan 2002), particularly due to this being their regular feeding time (Morgado et al. 2012). As such, active behaviours such as locomotion and feeding are likely to occur at a higher frequency in the morning and mid-afternoon than during the rest of the day. The expression of investigative behaviour during enrichment was notably lower than in tapir activity budgets from the literature (Gilmore 2007; Montenegro 1998), despite a 106.8% increase in the enrichment period. The most likely explanation for this is habituation (Anderson et al. 2010; Wells and Egli 2004). Despite the order of enrichment being randomised in this study, each was presented five times to the tapirs in the same manner. Thus, the novelty, and amount of investigation each enrichment type yielded, may have reduced over the experimental period.

Neither visitor numbers nor ambient temperature had a significant effect on the tapirs' behaviour in the baseline or experimental periods. This contrasts with research on visitor presence and tapir behaviour whereby captive tapir exhibited less activity while visitor numbers were high (Dutra and Young 2015) and 11.2% of activity variation due to climate (Gilmore 2007). During the study period, temperature varied between 16°C and 2°C, while visitor numbers ranged from 161 to 0, when the site was closed to the public. Both variables were within a relatively small range and may not have varied enough to influence behavioural diversity. Moreover, adverse environmental conditions (like extreme temperature or high public presence) have less impact on the behaviour and welfare of animals in suitable habitats (Sherwen and Hemsworth 2019). The tapirs' habitat exceeds guidelines on tapir husbandry (AZA Tapir TAG 2013) in terms of size and provisions of shelters and pools, which may mitigate the effects of temperature and visitor numbers (Sherwen and Hemsworth 2019).

Time spent out of sight did not change significantly between conditions, so changes in behaviour are not due to the animals being in sight more or less frequently. An important note, particularly with regards to resting and out of sight behaviours, is that the use of proportional data in this study means that an increase in one behaviour obliges others to decrease (Jaman and Huffman 2008). It may not be that nutritional enrichment causes less desire or need for rest but that it stimulates greater behavioural diversity in the hour after enrichment is provided, reducing the proportion of time dedicated to rest. Resting behaviour may simply have been delayed to later in the day whilst observations were not being conducted.

There were fewer significant differences between enrichment types than hypothesised. This could be a result of the study's small sample size, as applying multiple comparison corrections (like Bonferroni) increases the likelihood of type II error (Ranstam 2016). Indeed, the small sample size likely reduced the statistical power of the results (Hawkins 2009). This does not mean however that the importance of the findings in this study, and their possible implications for tapir welfare, should be dismissed (Plowman 2008; de Azevedo et al. 2007). Replication of the methodology in this study with larger sample sizes and 24-hour observations, with more enrichment designs installed in a greater portion of habitat space, would increase the positive predictive value of the findings and provide a wider understanding of the impact of enrichment on tapir.

## Conclusion

The tapirs in this study spent a higher proportion of time feeding after the provision of food-based enrichment compared to baseline behaviours, as well as compared with the provision of some sensory enrichments. Therefore, we suggest that food-based enrichments such as puzzle feeders should be incorporated into husbandry plans to increase the expression of feeding behaviours. The feed-based enrichments tested, had no impact on the proportion of observations animals spent resting or locomoting in the hour after enrichment was given in comparison to the baseline observations. Some sensory enrichment was more effective at increasing locomotion and resting behaviours compared with some feeding enrichments but did not impact behaviour compared to the baseline. As such, biologically relevant olfactory enrichment should be prioritised over other sensory enrichment and overall, a range of enrichments should be implemented to encourage a variety of behaviour. Tapirs' habitats can also be environmentally enriching, and should be designed to provide ample browsing opportunities, as well as structural resources which allow tapirs to mitigate the effects of adverse environmental conditions. Further research should quantify habituation in tapir to maximise enrichment efficacy and collect behavioural data over a longer time period after the implementation of enrichment. Finally, enrichment should be considered on an individual-specific level when designing tapir husbandry plans.

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## References

Anderson C., Arun A.S., Jensen P. (2010) Habituation to environmental enrichment in captive sloth bears—effect on stereotypies. *Zoo Biology* 29: 705–714. doi: 10.1002/zoo.20301

Andrade C. (2019) Multiple testing and protection against a Type 1 (false positive) error using the Bonferroni and Hochberg corrections. Indian *Journal of Psychological Medicine* 41: 99–100. doi: 10.4103/IJPSYM.IJPSYM_499_18

Arumugam K.A., Top M.M., Ibrahim W.N.W., Beusching C.D., Annavi G. (2020) Social and reproductive behavior of captive Malayan tapirs' (*Tapirus indicus*): Interactions with maternal experience and environmental conditions. *Scientific Reports* 10(4117): 1–9. doi: 10.1038/s41598-020-60429-0

AZA Tapir TAG (2013) *Tapir (Tapiridae) Care Manual.* Association of Zoos and Aquariums: Silver Spring, MD. pp, 65. https://nagonline.net/wp-content/uploads/2014/05/Tapir-ACM-2013-NAG-EDIT.pdf

Bashaw M.J., Bloomsmith M.A., Marr M.J., Maple T.L. (2002) To hunt or not to hunt? A feeding enrichment experiment with captive large felids. *Zoo Biology* 22(2): 103–198. doi: 10.1002/zoo.10065

Bates D., Maechler M., Bolker B., Walker S. (2014) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48. doi: 10.18637/JSS.V067.I01

Bateson M., Martin P. (2021) *Measuring Behaviour. An Introductory Guide*. 4th ed. Cambridge: Cambridge University Press.

Bishop J., Hosey G., Plowman A. (2013) *Handbook of Zoo & Aquarium Research.*

Brando S., Vitale A., Bacon M. (2023) Promoting good nonhuman primate welfare outside regular working hours. *Animals* 13(8): 1423. doi: 10.3390/ani13081423

Christensen J.W., Rundgren M. (2008) Predator odour per se does not frighten domestic horses. *Applied Animal Behaviour Science* 112: 136–145. doi: 10.1016/j.applanim.2007.08.003

Clark F., Miller L.J. (2015) Utilizing scents as environmental enrichment: Preference assessment and application with Rothschild Giraffe. *Animal Behavior & Cognition* 2(3): 285–291. doi: 10.12966/abc.08.07.2015

Clark F.E. (2017) Cognitive enrichment and welfare: Current approaches and future directions. *Animal Behavior & Cognition* 4(1): 52–71. doi: 10.12966/abc.05.02.2017

Clauss M., Wilkins T., Hartley A., Hatt J-M. (2009) Diet composition, food intake, body condition, and faecal consistency in captive tapirs (*Tapirus* spp.) in UK collections. *Zoo Biology* 28, 279–291. https://doi.org/10.1002/zoo.20225

Coe J. (2017) *Embedding Environmental Enrichment into Zoo Animal Facility Design.* Zoo Design Conference. Wroclaw Zoo, 5-7 April 2017, Wroclaw: Poland. https://zoolex.org/media/uploads/2018/07/29/coe_2017_environmental_enrichment_for_designers.pdf.

Crawley M.J. (2013) *The R Book. 2nd edition.* Chichester: John Wiley & Sons, Ltd.

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. doi: 10.1016/j.applanim.2006.05.034

Dutra L.M.L., Young R.J. (2015) Can enrichment make Brazilian tapir spend more time on view to the public? *Journal of Applied Animal Welfare Science* 18(1): 74–81. doi: 10.1080/10888705.2014.945177

Fábregas M.C., Guillén-Salazar F., Garcés-Narro C. (2012) Do naturalistic enclosures provide suitable environments for zoo animals? *Zoo Biology* 31: 362–373. doi: 10.1002/zoo.20404

Fernandez E.J., Upchurch B., Hawkes N.C. (2021) Public feeding interactions as enrichment for three zoo-housed elephants. *Animals* 11(6): 1689. doi: 10.3390/ani11061689

Ferrero B., Noriega J.I. (2007) A new tapir from the upper Pleistocene of Argentina: phylogenetic remarks on the neotropical family diversification and paleoenvironmental inferences. *Journal of Vertebrate Paleontology* 27(2): 504–511.

Finch K., Humphreys A. (2022) Day time activity budgets, height utilization and husbandry of two zoo-housed Goodfellow's tree kangaroos (*Dendrolagus goodfellowi buergersi*). *Journal of Zoological and Botanical Gardens* 3: 102–112. doi: 10.3390/jzbg3010009

Ghavamian Y., Minier D.E., Jaffe K.E. (2022) Effects of complex feeding enrichment on the behavior of captive Malayan sun bears (*Helarctos malayanus*). *Journal of Applied Animal Welfare Science* 25: 1–15. doi: 10.1080/10888705.2021.2023874

Gilmore M. (2007) Tapir behavior: An examination of activity patterns, mother-young interactions, spatial use, and environmental effects in captivity on two species (*Tapirus indicus* and *Tapirus bairdii*). MSc Dissertation, Oklahoma State University.

Glaeser, S.S., Shepherdson, D., Lewis, K., Prado, N., Brown, J.L., Lee, B., Wielebnowski, N. (2021) Supporting zoo Asian elephant (*Elephas maximus*) welfare and herd dynamics with a more complex and expanded habitat. *Animals* 11(9): 2556. doi: 10.3390/ani11092566

Gómez H., Wallace R., Ayala G., Tejada R. (2005) Dry season activity periods of some Amazonian mammals. *Studies on Neotropical Fauna and Environment* 40(2): 91–95. doi: 10.1080/01650520500129638

Guidelines for conducting research in zoos and aquariums. London: BIAZA.

Happ M., Bathke A.C., Brunner E. (2018) Optimal sample size planning for the Wilcoxon-Mann-Whitney test. *Statistics in Medicine* 38: 363–375. doi: 10.1002/sim.7983

Hatt J.M., Schaub D., Wanner M., Wettstein H.R., Flach E.J., Tack C., Hässig M., Ortmann S., Hummel J., Clauss M. (2005) Energy and fibre intake in a group of captive giraffe (*Giraffa camelopardalis*) offered increasing amounts of browse. *Journal of Veterinary Medicine Series A*, 52(10), 485-490.. doi: 10.1111/j.1439-0442.2005.00769.x

Hawkins D. (2009) Biomeasurement: *A student's guide to biological statistics. 2nd edition*. Oxford: Oxford University Press.

Herrera J.C., Taber A.B., Wallace R.B., Painter R.L.E. (1999) Lowland tapir (*Tapirus terrestris*) behavioral ecology in a southern Amazonian tropical forest. *Vida Silvestre Neotropical* 8(1-2): 31–37.

Hosey G., Melfi V., Pankhurst S. (2009) *Zoo Animals. Behaviour, Management and Welfare*. Oxford: Oxford University Press.

Hoy J.M., Murray P.J., Tribe A. (2010) Thirty years later: Enrichment practices for captive mammals. *Zoo Biology* 29: 303–316. doi: 10.1002/zoo.20254

Hurst J.L., Beynon R.J., Roberts T.D., Wyatt T.D. (2008) *Chemical Signals in Vertebrates*. New York: Springer.

Huskisson S.M. (2020) Species-Specific Behavior. In: Vonk J., Shackleford T. eds. *Encyclopedia of Animal Cognition and Behavior*. New York: Springer, Cham. https://link.springer.com/referenceworkentry/10.1007/978-3-319-47829-6_138-1?page=4

Inglis I.R., Langton S., Forkman B., Lazarus J. (2001) An information primacy model of exploratory and foraging behaviour. *Animal Behaviour* 62(3): 543–557. doi: 10.1006/anbe.2001.1780

Jaman M., Huffman M.A. (2008) Enclosure environment affects the activity budgets of captive Japanese macaques (*Macaca fuscata*). *American Journal of Primatology* 70(12): 1133–1144. doi: 10.1002/ajp.20612)

Kakol K.A. (2021) Environmental enrichment for zoo-housed Icelandic reindeer (*Rangifer tarandus*). MSc Dissertation, Linköping University.

Kinahan A.A. (2002) Addressing fundamental behavioural and welfare issues associated with zoo housed animals: using lowland tapirs *Tapirus terrestrius* and giraffes *Giraffa camelopardalis* as model species. Ph.D. Thesis: Trinity College (Dublin, Ireland).

Kleiman D.G., Thompson K.V., Baer C.K. (2010) *Wild Mammals in Captivity. Principles and Techniques for Zoo Management.* 2nd ed. Chicago: University of Chicago Press.

Laule G.E. (2002) Positive reinforcement and environmental enrichment: enhancing animal well-being. *Journal of the American Veterinary Medical Association* 223(7): 957–983

Machado J.C., Genaro G. 2014. Influence of olfactory enrichment on the exploratory behaviour of captive-housed domestic cats. *Australian Veterinary Journal* 92(12): 492–498. doi: 10.1111/avj.12253

Mahler A.E. (1984) Activity budgets and use of exhibit space by South American tapir (*Tapirus terrestris*) in a Zoological Park setting. *Zoo Biology* 3: 35–46. doi: 10.1002/zoo.1430030105

Marcordes S., Lueders I., Grund L., Sliwa A., Maurer F.P., Hillemann D., Möbius P., Barth S.A. (2020) Clinical outcome and diagnostic methods of atypical mycobacteriosis due to *Mycobacterium avium* ssp. *hominissuis* in a group of captive lowland tapirs (*Tapirus terrestris*). *Transboundary and Emerging Diseases* 68(3): 1305–1313. doi: 10.1111/tbed.13786

Martínez-Macipe M., Lafont-Lecuelle C., Pageat P., Cozzi A. (2023) Evaluation of an innovative approach for sensory enrichment in zoos: semiochemical stimulation for captive lions (*Panthera leo*). *Animal Welfare* 24(4): 455–461. doi: 10.7120/09627286.24.4.455

Mason G., Clubb R., Latham N., Vickery S. (2006) Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science* 102(3): 163–188.

Medici, E.P. (2014) Health assessment of wild lowland tapir (Tapirus terrestris) populations in the Atlantic forest and Pantanal biomes, Brazil (1996–2012). *Journal of Wildlife Diseases* 50(4): 817–828. doi: 10.7589/2014-02-029

Medici E.P. (2011) Family Tapiridae (Tapirs). In: Wilson D.E., Mittermeier R.A. eds. *Handbook of the mammals of the world, Hoofed mammals*. Barcelona: Lynx Editions, 182–204.

Mellor D.J., Beausoleil N.J., Littlewood K.E., McLean A., McGreevy P.D., Jones B., Wilkins C. (2020) The 2020 Five Domains Model: Including human-animal interactions in assessments of animal welfare. *Animals* 10(10): 1870. doi: 10.3390/ani10101870

Mkwanazi M.V., Ncobela C.N., Kanengoni A.T., Chimonyo M. (2019) Effects of environmental enrichment on behaviour, physiology and performance of pigs — A review. Asian-Australasian *Journal of Animal Science* 32(1): 1–13. doi: 10.5713/ajas.17.0138

Montenegro O.L. (1998) The behavior of lowland tapir (*Tapirus terrestris*) at a natural mineral lick in the Peruvian Amazon. Msc Thesis: University of Florida.

Morgado E., Juárez C., Melo A.I., Domínguez B., Lehman M.N., Escobar C., Meza E., Caba M. (2012) Artificial feeding synchronizes behavioral, hormonal, metabolic and neural parameters in mother-deprived neonatal rabbit pups. *European Journal of Neuroscience* 34(11): 1807–1816. doi: 10.1111/j.1460-9568.2011.07898.x

Noss A.J., Cuéllar R.L., Barrientos J., Maffei L., Cuéllar E., Arispe R., Rúmiz D., Rivero K. (2003) A camera trapping and radio telemetry study of Lowland tapir (*Tapirus terrestris*) in Bolivian dry forests. *Newsletter of the IUCN/SSC Tapir Specialist Group* 12: 24–32.

Oliveira-Santos L., Machado-Filho L., Tortato M., Brusius L. (2009) Influence of extrinsic variables on activity and habitat selection of lowland tapirs (*Tapirus terrestris*) in the coastal sand plain shrub, southern Brazil. *Mammalian Biology* 75: 219–226. doi:10.1016/j.mambio.2009.05.006

Plowman A.B. (2008) BIAZA Statistics Guidelines: Toward a common application of statistical tests for zoo research. *Zoo Biology* 27(3): 226–233. doi: 10.1002/zoo.20184

Podlesnik C.A., Jimenez-Gomez C. (2016) Contrafreeloading, reinforcement rate, and behavioral momentum. *Behavioural Processes* 128: 24–28. doi: 10.1016/j.beproc.2016.03.022

R Core Team. (2019) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Ranstam J. (2016) Multiple P-values and Bonferroni correction. *Osteoarthritis and Cartilage* 24: 763–764. doi: 10.1016/j.joca.2016.01.008

Rose P., Robert R. (2013) Evaluating the activity patterns and enclosure usage of a little-studied zoo species, the sitatunga (*Tragelaphus spekii*). *Journal of Zoo and Aquarium Research* 1: 14–19. doi: 10.19227/JZAR.V1I1.12

Rose, P.E., Roffe, S.M. (2012) A case study of Malayan tapir (*Tapirus indicus*) husbandry practise across 10 zoological collections. *Zoo Biology* 32(3): 347–356. doi: 10.1002/zoo.21018

Rose, P., Roffe, S.M. (2008) The effect of enrichment on activity budgets of Malayan tapir (*Tapirus indicus*) at the East Midland Zoological Society: Twycross Zoo. *BIAZA Research Newsletter* 9(5).

Rose P., Roffe S., Jeremy M. (2006) Enrichment methods used for Tapirus indicus (*Malayan tapir*) at The East Midland Zoological Society: Twycross Zoo. *RATEL* 33(4): 8–13.

Sasson-Yenor, J., Powell, D.M. (2019) Assessment of contrafreeloading preferences in giraffe (*Giraffa camelopardalis*). *Zoo Biology* 38(5): 414–423. doi: 10.1002/zoo.21513

Schipper L.L., Vinke C.M., Schilder M.B.H., Spruijt B.M. (2008) The effect of feeding enrichment toys on the behaviour of kennelled dogs (*Canis familiaris*). *Applied Animal Behaviour Science* 114(1–2): 182–195. doi: 10.1016/j.applanim.2008.01.001

Sha J.C.M., Ismail R., Marlena D., Lee, J.L. (2016) Environmental complexity and feeding enrichment can mitigate effects of space constraints in captive callitrichids. *Laboratory Animals* 50(2): 137–144. doi: 10.1177/0023677215589258

Sherwen S.L., Hemsworth P.H. (2019) The visitor effect on zoo animals: Implications and opportunities for zoo animal welfare. *Animals* 9(6): 366. doi: 10.3390/ani9060366

Sherwen S.L., Hemsworth P.H., Butler K.L., Fanson K.V., Magrath M.J.L. (2015) Impacts of visitor number on Kangaroos housed in free-range exhibits. *Zoo Biology* 34(4): 287–295. doi: 10.1002/zoo.21226

da Silva A.G., Lalonde D.R., Quse V., Shoemaker A., Russello M.A. (2010) Genetic approaches refine ex-situ Lowland tapir (*Tapirus terrestris*) conservation. *Journal of Heredity* 101(5): 581–590. doi: 10.1093/jhered/esq055

Stoinsky T.S., Daniel E., Maple T.L. (2000) A preliminary study of the behavioral effects of feeding enrichment on African elephants. *Zoo Biology* 19(6): 485–554. doi: 10.1002/1098-2361(2000)19:6<485::AID-ZOO1>3.0.CO;2-5

Swaisgood R., Shepherdson D. (2008) Environmental enrichment as a strategy for mitigating stereotypies in zoo animals: a literature review and meta-analysis. In: Mason, G., Rushen, J. eds. *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*. (2nd edition.). Oxford: Oxford University Press, 225-285.

Swaisgood R.R., White A.M., Zhou X., Zhang G., Lindburg D.G. (2005) How do giant pandas (*Ailuropoda melanoleuca*) respond to varying properties of enrichments? A comparison of behavioral profiles among five enrichment items. *Journal of Comparative Psychology* 119(3): 325–334.

De Thoisy B., Da Silva A.G., Ruiz-García M., Tapia A., Ramirez O., Arana M., Quze V., Paz-y-Miño C., Tobler M., Pedraza C., Lavergne A. (2010). Population history, phylogeography, and conservation genetics of the last Neotropical mega-herbivore, the lowland tapir (*Tapirus terrestris*). *BMC Evolutionary Biology*, 10, 1-16. doi: 0.1186/1471-2148-10-278

Tremblay A. (2020) *LMERConvenienceFunctions: Model Selection and Post-Hoc Analysis for (G)LMER Models*. R package version 3.0. https://CRAN.R-project.org/package=LMERConvenienceFunctions.

Tsuchiya Y., Yayota M., Kashima Y., Shiota Y. (2023) Nutritional effect of feeding enrichment using bamboo *Pleioblastus* in zoo-kept Asian elephants *Elephas maximus. Journal of Zoo and Aquarium Research* 11(2): 267–273. doi: 0.19227/jzar.v11i2.686267

Van de Pol M., Wright J. (2009) A simple method for distinguishing within-versus between-subject effects using mixed models. *Animal Behaviour* 77(3): 753–758. doi: 10.1016/j.anbehav.2008.11.006

Varela D., Flesher K., Cartes, J.L., de Bustos S., Chalukian S., Ayala G., Richard-Hansen C. (2019) *Tapirus terrestris. The IUCN Red List of Threatened Species* 2019. Available at: https://www.iucnredlist.org/species/21474/45174127.

Veasey J., Hammer G. (2010) Managing captive mammals in mixed-species communities. In: Kleiman D.G., Thompson K.V., Baer C.K. (eds). *Wild Mammals in Captivity. Principles and Techniques for Zoo Management*. 2nd ed. Chicago: University of Chicago Press.

Veeraselvam M., Sridhar R., Jayathangaraj M.G., Perumal P. (2013) Behavioural study of captive sloth bears using environmental enrichment tools. *International Journal of Zoology* 2013: 1–6. doi: 10.1155/2013/526905

Wells D.L. (2009) Sensory stimulation as environmental enrichment for captive animals: A review. *Applied Animal Behaviour Science* 118(1-2): 1–11. doi: 10.1016/j.applanim.2009.01.002

Wells D.L., Egli J.M. (2004) The influence of olfactory enrichment on the behaviour of captive black-footed cats, *Felis nigripes*. *Applied Animal Behaviour Science* 85 107–119. doi: 10.1016/j.applanim.2003.08.013

White B.C., Houser L.A., Fuller J.A., Taylor S., Elliott L.L. (2003) Activity-based exhibition of five mammalian species: Evaluation of behavioural changes. *Zoo Biology* 22: 269–285.

Yeates J.W., Main D.C.J. (2008) Assessment of positive welfare: a review. *The Veterinary Journal* 175(3): 293–300. doi: 10.1016/j.tvjl.2007.05.009

Zayonc D., Coomes O.T. (2021) Who is the expert? Evaluating local ecological knowledge for assessing wildlife presence in the Peruvian Amazon. *Conservation Science and Practice* 4(2): 600. doi: 10.1111/csp2.600

Zobel G., Nawroth C. (2020) Current state of knowledge on the cognitive capacities of goats and its potential to inform species-specific enrichment. *Small Ruminant Research* 192: 106208. doi: 10.1016/j.smallrumres.2020.106208