



Article

A Comparison of Food and Non-Food Enrichment with Zoo-Housed African Lions (*Panthera leo*)

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Abstract: Ongoing research on the effectiveness of enrichment at the species, group, and individual levels is beneficial to our growing understanding of animal welfare and behaviour for animals housed in human care. Diversifying the enrichment opportunities offered to animals in facilities such as zoos and aquariums helps to encourage a wide repertoire of species-typical, naturalistic, and rewarding behaviours. The present study aimed to examine the behavioural impact of novel food (ice blocks, gelatine, eggs) and non-food (lavender, clean sheets, mirrors) enrichment strategies on two zoo-housed prides of African lions (*Panthera leo*) housed in a rotation-based enclosure system at Orana Wildlife Park, New Zealand. The results of the study indicate that, while both forms of enrichment had a behavioural impact, the effects on behaviour varied with the type of enrichment used, both between and within the two categories. Different enrichment strategies varied in their impacts on resting behaviour, locomotion, and exploration levels in the lions. An increased focus on the specific behavioural outcomes of various novel enrichment strategies is essential to expand the efficacy of enrichment programs for future efforts to improve the wellbeing of zoo-housed animals.



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1. Introduction

The African lion (*Panthera leo*) is a familiar and popular carnivore species found in many zoos worldwide. A primary challenge for caregivers is that zoo environments often lack the complexity of wild habitats, limiting opportunities for animals to exhibit a full range of natural behaviours [1]. As wide-ranging carnivores, lions are particularly susceptible to developing stereotypic behaviours in less stimulating environments [2,3]. To address these issues, zoos worldwide continuously work to refine care practices, incorporating diverse environmental enrichment strategies that promote diverse behavioural repertoires and positive welfare states [4]. In particular, there should be a focus on encouraging functional behaviours or behaviours which are intended to achieve a specific goal, irrespective of whether they are considered wholly natural.

Enrichment aims to create opportunities for animals to display a naturalistic activity budget with a variety of rewarding behaviours [5]. Active animals engaging in a diverse array of naturalistic and functional behaviours not only contribute to a more engaging

visitor experience [6] but also benefit from improved wellbeing. Mellor et al. [7] emphasises that welfare management should reduce survival-critical states while facilitating rewarding behaviours. Mellen and MacPhee [8] advocate for defining enrichment based on each individual animal's needs and natural histories, aligning with Poole's [9] principles of security, complexity, achievement, and novelty. Contemporary care programs have integrated these concepts, emphasising complexity, choice, and control in captive [10]. Despite progress, significant opportunities remain to diversify enrichment offerings [11].

Systematic research and feedback on the efficiency of different strategies are essential to ensure that the goals of environmental enrichment are met in the target species [12]. However, the effectiveness of enrichment is not always uniform; not all interventions equally reduce stereotypic behaviours, and the effects can vary across species [13]. In a study of squirrel monkeys (*Saimiri sciurius*), enrichment interventions did not consistently reduce stereotypical behaviour in all individuals, suggesting that enrichment may also vary in its impact on individuals [14]. Inconsistencies in defining stereotypic behaviours and enrichment types complicate the understanding of effective strategies [13]. Brereton and Rose [11] also note a bias towards nutrition-based enrichment in the literature, despite evidence which supports the incorporation of a broader array of strategies.

While the performance of natural behaviour is commonly used as a criterion in the determination of animal welfare, some natural interactions with the environment may decrease welfare, whereas some unnatural interactions increase it. Browning [15] posits that natural functioning is neither necessary nor sufficient for understanding welfare, suggesting a shift towards assessing behavioural preferences and enjoyment instead. This approach encourages the recreation of rewarding behaviours observed in the wild and which is based on biological evidence [11] and which uses both enclosure design and dynamic enrichment items. For instance, common enrichment strategies provided to felids, such as bungee ropes, artificial prey and feeding poles, are designed following this principle by providing large carnivores with the opportunity to jump, climb and use their strength to grab "prey", mimicking their natural hunting behaviours with artificial objects. Of course, these items are not 'natural'; a lion would not encounter bungee ropes in the wild. The goal is that normal behaviours with a specific function are encouraged, regardless of whether the means to achieve that behaviour is a natural or unnatural object. Providing felids with enrichment has been shown to positively affect activity levels [14–18] and reduce non-functional and abnormal stereotypic behaviours [14,16,19–22]. For example, feeding poles have been linked to lower arthrosis rates and reduced body fat in tigers (*Panthera tigris*) [23].

Many commonly used enrichment strategies focus primarily on food rewards, leading to the prevalence of nutrition-based approaches compared with other enrichment types [11]. In the wild, lions are only successful at hunting 40% of the time [24]. Consequently, while appetitive behaviours make up a considerable proportion of their behavioural repertoire [16], they do not always result in food rewards. Understanding the intrinsic motivations underlying animal behaviour is crucial for predicting the effectiveness of enrichment strategies and varying enrichment to include opportunities for intermittent rewards. Of course, failing to meet appetitive drives can lead to frustration when their motivations are not fulfilled. This does not mean that a non-reward is the same as causing distress. Arousal and exploration are in themselves part of appetitive behaviour repertoires, driven by stimuli that animals 'want' to explore [25]. The context of the animals' internal experience should inform best practice; the provision of sensory non-food enrichment, for example, could be used to encourage appetitive behaviours motivated by states other than hunger and thirst which do not necessarily need to be rewarded through consummatory behaviour.

Tarou and Bashaw [26] highlight that animals are intrinsically motivated to explore novel objects, indicating that different enrichment classes elicit diverse exploratory be-

haviours where satisfying curiosity is a reward in itself. For example, adding sensory stimuli, such as herbs, flowers, blood, perfumes, and other scents, to a familiar environment can be utilised to add novelty and encourage sensory behaviours in big cats [27–29]. Novel visual enrichment strategies, such as sensory illusions [30] can also stimulate attentive and exploratory behaviours which mimic hunting-related activities. Unfortunately, scientifically backed evidence supporting the effectiveness of non-food interventions in felids is scarce, and in their review of enrichment for tigers, Szokalski et al. [29] emphasised the need for further contemporary research in this area. Historically, studies which examined the benefits of enrichment in zoo animals focused largely on a reduction in ‘negative’ state behaviours, and less so on the specific behaviours encouraged by different enrichment types and the positive impacts these behaviours have on the animal’s welfare state.

Fernandez and Martin [31] recently critiqued zoo-based environmental enrichment and recommended that, by monitoring an individual or a group’s enrichment usage across different conditions, the effectiveness of enrichment programmes could be increased by incorporating factors including preference, variation, and choice. In the same review, the authors highlighted that, with typically small sample sizes and an individual-focused approach to management, zoos are well positioned for studies which examine the functional relationship between variables. Traditionally, enrichment for animals has been selected based on the opinions of keepers and shared anecdotes of success [32]. There is potential for the incorporation of a systematic basis for the selection of enrichment items, although this has been suggested by only a handful of researchers over the past two decades [8,32,33]. Such an approach requires individual-focused, data-driven enrichment evaluation. However, many caregivers lack time or resources for thorough documentation [34]. Thus, zoo studies evaluating the effects of various enrichment types on behaviour and welfare provide an invaluable resource for animal caregivers.

In this study, we aimed to compare the short-term effects of enrichment with various novel foods (ice blocks, gelatine, and eggs) and non-foods (lavender, sheets, and mirrors) on the behaviour of zoo-housed African lions. These lions were accustomed to receiving enrichment as a regular part of their daily management but had not previously been given these specific items. Our research serves as an exploratory study of the behavioural changes induced by these enrichment types, providing valuable data for zoo and aquarium caregivers. By understanding how these enrichments can effectively influence felid behaviour, we hope to add to the growing area of literature that informs the implementation of enrichment practices for goal-based enrichment programs.

2. Materials and Methods

2.1. Subjects and Housing

This study was conducted at the Orana Wildlife Park in Christchurch, New Zealand, from 2010 to 2011. The subjects included 12 of the 13 lions housed between two separate prides (see Table 1). One lion in Priscilla’s pride, Meeka, was excluded because of her pregnancy during the study.

Table 1. Subject information for all lions in the study conducted from 2010 to 2011.

Pride	Lion	Sex/Birth Year	Relation
Pride 1 (Priscilla’s pride)	Priscilla	Female/1998	Pride leader
	Rah	Male/2004	Son of Priscilla Castrated
	Leah	Female/2005	Daughter of Priscilla

Table 1. *Cont.*

Pride	Lion	Sex/Birth Year	Relation
Pride 2 (Kiara's pride)	Kiara	Female/1998	Former pride leader
	Mishka	Female/2004	Current pride leader, Daughter of Kiara
	Sakura	Male/2005	Son of Kiara, castrated
	Kahn	Male/2005	Son of Kiara, castrated
	Toa	Male/2009	Son of Kiara, vasectomized during study
	Tawhiri	Male/2009	Son of Kiara, castrated
	Kairangi	Male/2009	Son of Kiara, castrated
	Tua	Female/2009	Daughter of Mishka
	Tama	Female/2009	Daughter of Mishka

The two lion prides were housed separately in large outdoor areas. Priscilla's pride (Group 1) was housed in a 4500 m² outdoor area during this study, and Kiara's pride (Group 2) was housed in a 5400 m² outdoor area during this study. Both enclosures consisted of large open grassed areas with sporadic clusters of large trees providing shade. The enclosures also had large rocks for the lions to use as resting spots or outlook over the enclosures. In the enclosure that houses Kiara's pride, there was a gravelled, looped road which was used for a "lion-encounter truck," which itself was used to bring park visitors into the enclosures for close-up feeding encounters which were executed by trained lion caretakers. While the lions did not change enclosures during the duration of the study, the lions at Orana are housed in a rotation-based system wherein both prides are regularly switched between the outdoor areas. Both outdoor areas consist of natural trees, deadfalls, grass, and rocks. Both areas were connected by an off-exhibit area, where all lions were housed at night or when they were not on exhibit. Each group had contact with their pride, whereas in the off-exhibit areas, they did not have direct contact with the other pride. Feeding and other forms of novel enrichment were routinely provided in the form of scatter feeds or extra feedings, both on and off the exhibit areas. Lions were typically released into their exhibited outdoor area between 08:00 and 09:00 h and moved into their off-exhibit areas between 17:00 and 18:00 h.

The normal feeding routine of lions revolved around a Lion Truck Feed that was performed daily at 14:30 h in an outdoor area. The Lion Truck Feed is a public feed where a modified truck with a cage takes zoo visitors into the lion's exhibited area, and keepers provide 5 kg horse meat in small portions to the lions. At the end of the truck feed encounter, the lions were provided a bone treat. Individual diet portions were fed at the end of the day to lions that had experienced the lion truck feed, so correct quantities of food could be provided to all individual animals. The amount fed depended on the individual but varied from 5 kg to 10 kg. The Lion Truck Feed rotated every other day between the two prides, with the pride not experiencing the Lion Truck Feed and therefore having a fasting day. Daily routine was performed with both prides.

2.2. Materials

Materials included enrichment items used during the enrichment conditions of the study (see below), a 16 GB Cowon © S9 digital AV player for voice-recorded observations

(Cowon Systems, Inc., Seoul, Republic of Korea), and a Sanyo © X1220 12.1-megapixel digital camera (Sanyo Electric Co., Ltd., Moriguchi, Osaka, Japan) for video-recorded observations. Other materials included data sheets and Excel files, and all observations were later transcribed.

2.3. Design and Procedure

Prior to its implementation, the study was approved by the administration at Orana Wildlife Park and the University of Applied Sciences Van Hall Larenstein. An ethogram consisting of 25 behaviours split into eight classes of behaviours was also developed prior to the implementation of the study (see Table 2). The behaviours observed were mutually exclusive, and the inclusion of the “Other” observation category made the ethogram exhaustive. For the entire data collection process, a focal, continuous sampling method was used to record all behaviours from the video. Observations were 60 min long for each lion, beginning immediately following the release of the lions between 08:00 and 09:00 h.

Table 2. Class of behaviours and definitions for each response in the ethogram.

Class	Behaviour	Definition
Locomote	Walking	Moving slowly
	Running	Moving fast
	Jumping	At least two paws leave the ground
	Rolling/stretching	Extended reach while lying down
Rest	Sitting	Backside on ground, while upright
	Lying Down	At least one side on ground
	Standing	Upright with no movement
	Bathing	Non-drinking contact with water
Stereotypy	Pacing	Repetitive movement; at least one back-and-forth loop
Explore	Sniffing	Head lifted while inhaling
	Digging	Using paws to move dirt
	Interacting with object	Any contact with moveable objects (other than study enrichment)
	Interacting with enrichment	Contact with experimental enrichment item, including eating of food-based enrichment items
Eat	Eating	Mouth contact with edible food items, excluding consumption of enrichment items
	Drinking	Mouth contact with water (non-bathing)
Social	Interacting with other lion	Any contact with another lion
	Vocalising	Sound made by a lion, typically directed at another lion
	Stalking	Crouched hunting position directed at another lion
	Grooming	Licking/pawing body of self or conspecific

Table 2. *Cont.*

Class	Behaviour	Definition
Territorial	Scratch marking	Claw contact with non-movable structure
	Scent marking	Urine directed at a non-movable structure
	Rubbing	Face/body contact with non-movable structure
Other	Urinate/defecate	Non-directed excretion
	Out of sight	Not visible
	Other	Behaviour that does not meet above criteria

The study included an ABA reversal design between baseline (BL) and enrichment (food [F] and non-food [NF]) conditions as well as an alternating treatment design within the enrichment conditions. Baseline observations, where no additional novel enrichment was introduced to the enclosure, occurred for four days prior to and two days following the introduction of the enrichment conditions (see Table 3). Food and non-food enrichment conditions were alternated on different days, with a four-day break in the middle of the study, where enrichment was provided by zoo staff, but no measurements were taken. The enrichment used in this study was designed to be new and novel to the prides, while enrichment provision was a normal part of the daily routine at Orana Wildlife Park prior to and following the study. The enrichment items used in this study were largely novel to lions and have not been seen before. Each enrichment condition lasted for one day, and enrichment items were placed on the exhibit prior to the release of each pride. No other normally available enrichment items/procedures (e.g., scatter feeds) were made available during baseline or enrichment conditions, and while usually housed and managed on a rotation schedule, for the baseline and enrichment periods, the two prides were kept in the same enclosures to avoid bias (i.e., Kiara's pride > LR1; Priscilla's pride > LR2). The entire study was conducted across 16 consecutive days for each pride, with each pride's 16 days of study occurring between 16 November 2010 and 8 February 2011.

Table 3. Day, condition, type, and description of all events.

Days	Condition	Type	Description
1 to 4	Baseline	N/A	No additional enrichment used beyond daily lion truck feed
5	Food Enrichment	Ice Blocks	4 L of fresh blood mixed with water for 4 kg frozen blocks. Pride 1 received 3 blocks and pride 2 received 5 blocks
6	Non-Food Enrichment	Mirrors	2 mirrors per pride were tied at head height outside of enclosures
7 to 10	Not Tested	N/A	Varied enrichment, not directly tested
11	Food Enrichment	Gelatine	3 L fresh blood mixed with 125 g of gelatine (frozen moulds). Pride 1 received 3 moulds and pride 2 received 6 moulds
12	Non-Food Enrichment	Lavender	20 fresh lavender branches per exhibit scattered in each enclosure

Table 3. Cont.

Days	Condition	Type	Description
13	Non-Food Enrichment	Clean Sheet	Non-scented, clean sheet tied to a tree/trunk, one in each exhibit
14	Food Enrichment	Eggs	10 hard-boiled eggs per exhibit scattered in each enclosure
15 to 16	Baseline	N/A	No additional enrichment used.

2.4. Statistical Analyses

SigmaStat[®], version 11.0 (Systat Software Inc., San Jose, CA, USA) was used to perform all statistical analyses. When Shapiro–Wilk tests for normality and/or equal variance failed, nonparametric tests (described below) were used to conduct statistical analyses. Mann–Whitney rank sum tests were used to compare differences between each class of behaviour in the baseline periods before or after the enrichment conditions (before: 4 days $\times$ 12 lions = 48; after: 2 days $\times$ 12 lions = 24). Kruskal–Wallis analysis of variance (ANOVA) on ranks tests were used to examine differences between each class of behaviour during the baseline, food enrichment, and non-food enrichment conditions. When significant differences ($p < 0.05$) for the ANOVAs were found, post-hoc pairwise comparisons (using Dunn’s method) were implemented. Within each enrichment condition (food and non-food), differences between each class of behaviour during the three enrichment types (food = ice blocks, gelatine, and eggs; non-food = mirrors, lavender, and sheet) were compared using repeated-measures ANOVAs (parametric) or Friedman repeated-measures ANOVAs on ranks (nonparametric), with subject as the blocking factor. When significant differences ($p < 0.05$) for the ANOVAs were found (only occurred for the parametric tests run), post-hoc pairwise comparisons (using Holm–Sidak’s method) were implemented. Finally, descriptive statistics were reported in terms of mean (M) and standard error of the mean (SE).

3. Results

No significant differences ($p > 0.05$) were observed between the two baseline periods; therefore, all baseline observations were combined for all other comparisons. Figure 1 shows the activity budgets for all eight classes of behaviour across the baseline (BL), food enrichment (F), and non-food enrichment (NF) conditions. The specific numbers, as well as significant differences for the classes of behaviour between conditions, are listed in the next section.

3.1. Significant Differences Between Conditions

Table 4 shows the change across the three conditions for all eight classes of behaviours. There was a significant difference in locomote between the three conditions ($X^2_2 = 19.458$, $p < 0.001$). The food and non-food enrichment conditions were significantly lower compared with baseline ($p < 0.05$ for both). There was also a significant difference in rest between the three conditions ($X^2_2 = 36.896$, $p < 0.001$). The food and non-food enrichment conditions were significantly lower compared with baseline ($p < 0.05$ for both). There was a significant difference in stereotypy between the three conditions ($X^2_2 = 6.214$, $p < 0.045$). However, there were no post-hoc significant differences between the three conditions. There was a significant difference in explore between the three conditions ($X^2_2 = 100.152$, $p < 0.001$). The food and non-food enrichment conditions were significantly higher compared with baseline ($p < 0.05$ for both). Finally, there was a significant difference in territorial behaviours between the three conditions ($X^2_2 = 7.546$, $p < 0.023$). The food enrichment condition was significantly lower compared with the non-food enrichment condition ($p < 0.05$).

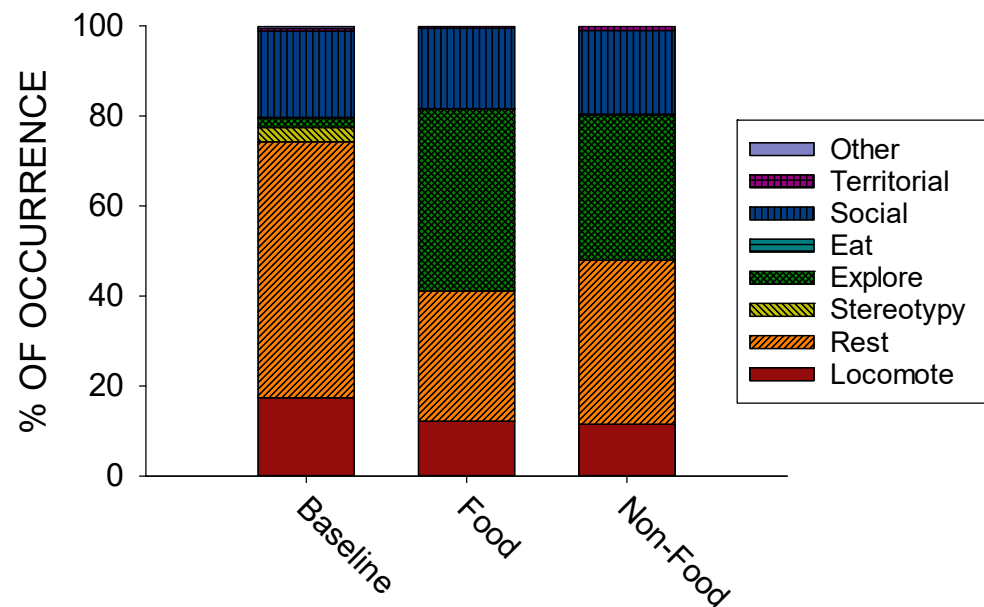


Figure 1. Activity budgets for all eight classes of behaviour across the three conditions (baseline, food enrichment, and non-food enrichment).

Table 4. Mean (with standard error of the mean) for each behaviour class across all three conditions. Significant differences are noted by differences in letters (*a* to *b*).

Behavior Class	Baseline	Food	Non-Food
Locomote	17.42 (± 0.88) ^a	12.19 (± 1.34) ^b	11.50 (± 0.79) ^b
Rest	56.86 (± 2.71) ^a	28.93 (± 2.51) ^b	36.44 (± 3.92) ^b
Stereotypy	3.178 (± 1.29)	0	0
Explore	2.12 (± 0.74) ^a	40.51 (± 3.57) ^b	32.31 (± 3.43) ^b
Eat	0.12 (± 0.06)	0.03 (± 0.03)	0.17 (± 0.09)
Social	19.15 (± 2.52)	17.85 (± 2.46)	18.60 (± 2.01)
Territorial	0.61 (± 0.07)	0.47 (± 0.10) ^a	0.98 (± 0.16) ^b
Other	0.54 (± 0.29)	0.03 (± 0.03)	0

3.2. Significant Differences Between Enrichment Types

Figure 2 shows the day-to-day activity for four of the classes of behaviours (locomote, rest, explore, and social) across all three conditions, including differences between the specific types of enrichment within each condition.

3.2.1. Enrichment Type and Locomote

For locomote, there was a significant difference between the three different types of food enrichment ($F_{2,22} = 13.704$, $p < 0.001$). Locomote was significantly higher during eggs enrichment compared with ice blocks and gelatine ($p < 0.05$ for both). There was also a significant difference between the three types of non-food enrichment ($F_{2,22} = 9.578$, $p < 0.001$). Locomote was significantly higher during lavender enrichment compared with sheets and mirrors ($p < 0.05$ for both).

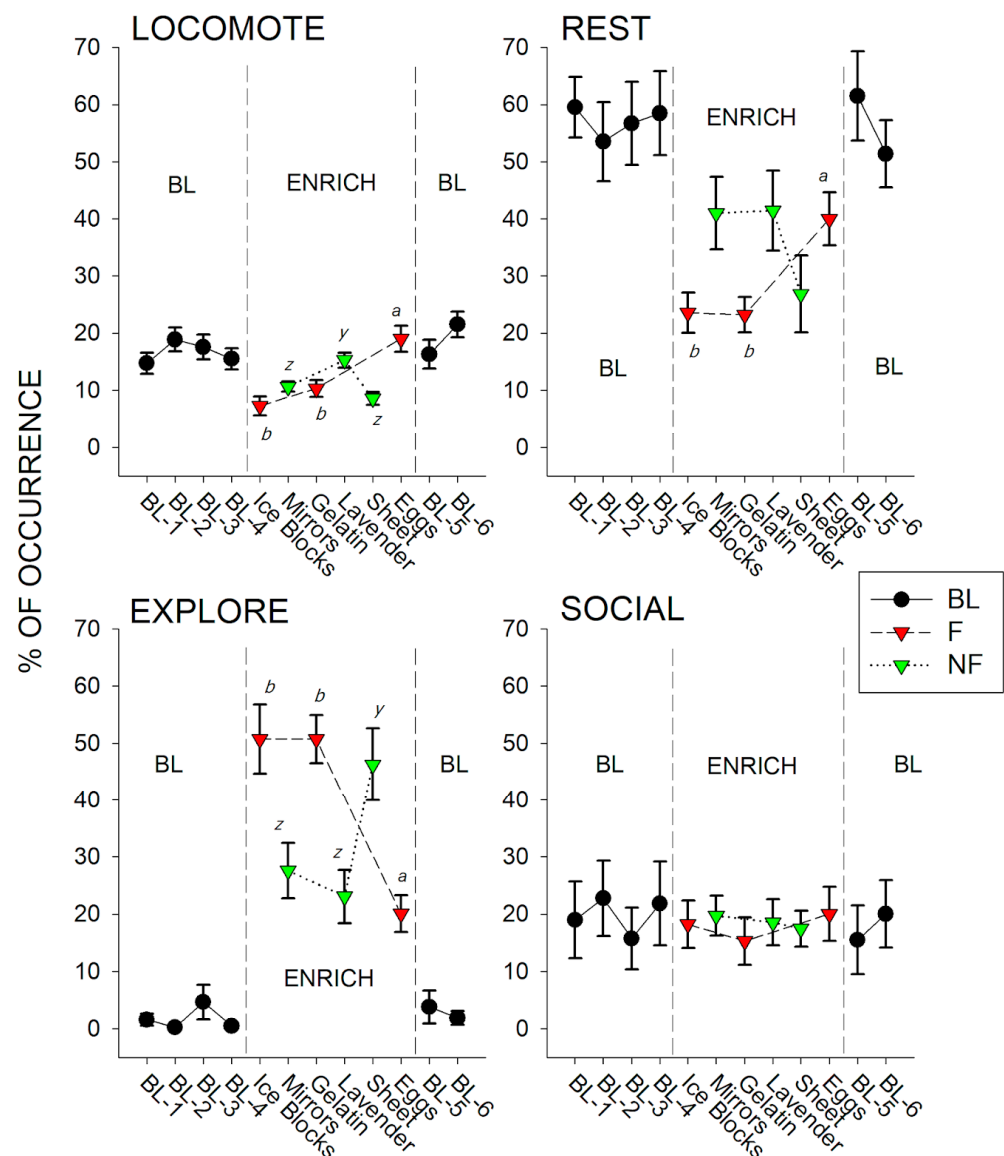


Figure 2. Average day-by-day activity (with standard error of the mean bars) for four of the classes of behaviour (locomote, rest, explore, and social). Each graph represents the ABA reversal design for the baseline (BL) and enrichment (Enrich) phases, with the alternating-treatment design between the food enrichment (F) and non-food enrichment (NF) conditions during the Enrich phase. Significant differences ($p < 0.05$) within the F and NF conditions are shown by differences between letters ($a-b$ or $y-z$).

3.2.2. Enrichment Type and Rest

For rest, there was a significant difference between the three different types of food enrichment ($F_{2,22} = 6.695$, $p < 0.005$). Rest was significantly higher during eggs enrichment compared with ice blocks and gelatine ($p < 0.05$ for both). There was also a significant difference between the three types of non-food enrichment ($F_{2,22} = 3.475$, $p = 0.049$). However, there were no post-hoc significant differences between the three enrichment types.

3.2.3. Enrichment Type and Explore

For explore, there was a significant difference between the three different types of food enrichment ($F_{2,22} = 17.853$, $p < 0.001$). Explore was significantly lower during eggs enrichment compared with ice blocks and gelatine ($p < 0.05$ for both). There was also a significant difference between the three types of non-food enrichment ($F_{2,22} = 5.514$,

$p < 0.011$). Explore was significantly higher during sheets enrichment compared with lavender and mirrors ($p < 0.05$ for both).

3.2.4. Enrichment Type and Territorial

For territorial behaviours, there was a significant difference between the three different types of food enrichment ($F_{2,22} = 5.191$, $p < 0.014$). Territorial behaviours were significantly higher during the enrichment with eggs, compared with ice blocks ($p < 0.05$). There was also a significant difference between the three types of non-food enrichment ($F_{2,22} = 6.477$, $p = 0.006$). Territorial behaviours were significantly higher during lavender enrichment compared with sheets and mirrors ($p < 0.05$ for both).

4. Discussion

The results of this study demonstrate that locomotion, rest, exploration, and stereotyped behaviours in lions were variably affected by the novel food and non-food enrichment techniques. Under both types of novel enrichment conditions, lions spent significantly less time locomoting and resting compared with the baseline and significantly more time engaging in territorial and exploratory behaviours. Overall, while the results indicate that food and non-food enrichment are equally effective enrichment strategies for lions, the effects on behaviour were variable not only between categories but also within them. The resultant increase in behavioural diversity associated with enrichment, as well as increased activity, is beneficial for the wellbeing of lions living in zoos [5] and may improve educational outcomes for visitors [6]. These behavioural impacts are categorised and discussed below as follows: (1) activity, (2) exploration, (3) stereotypic pacing and (4) territorial.

4.1. Activity

For both food and non-food enrichment, the lions spent significantly less time performing locomotive and resting behaviours compared with the baseline, where no additional enrichment was provided. While a decrease in movement might, at face value, be associated with a decrease in overall activity, which in turn contrasts with previous findings on the topic [16–18], it is more likely that this effect is the result of the lions spending more time engaging in other active behaviours, such as exploration of the enrichment items themselves, as opposed to representing an overall decrease. This is supported by the significant decrease in the time spent resting, which is consistent with the existing literature on enrichment for large felids [16–18]. It is essential to examine the possible impacts of both the items and their presentation when comparing the effects of different strategies on the lion's behaviour. Locomotion may have been higher during the eggs enrichment when compared with the ice blocks and the gelatine, for example, because the eggs were scattered around the enclosure and thus the lions would need to actively explore and move around to find them; the same can be said of the lavender, which was displayed in the same way. In contrast, the other forms of enrichment were either in a fixed location (sheets and mirrors) or large enough that the lions were likely to remain in one place while eating or licking them (ice blocks and gelatine). Rest may have been higher during the eggs enrichment as they were smaller and quicker to eat for a large carnivore, and so all the eggs were eaten faster than the ice and gelatine blocks were. Furthermore, the amount of gelatine and ice blocks was adjusted to the size of the pride, whereas the number of eggs was not, which may also account for why the eggs may have been eaten more quickly. Therefore, when planning and preparing enrichment programs, there is reason to consider not only the form of enrichment given, but also the way it is presented. For example, it would be useful to understand if the behaviour of the lions would have differed if the eggs and the lavender were provided in one location rather than scattered throughout the enclosure, as scatter

feeding is known to have varying impacts on animal behaviour, such as increasing the duration and frequency of foraging behaviour [35–37] and increasing enclosure use [38].

It is worth discussing that free-living lions spend most of their time resting, around 20 h per day, at levels comparable to what has been measured for lions living in zoos [3,39]. Although high levels of inactivity are often considered undesirable in zoo-living wild animals, acceptable levels must be considered at the species level in relation to their natural metabolism and energy expenditure. Lions living in the wild utilise most of their energy reserves for hunting and spend much of their time inactive to maintain their energy [39,40]. However, lions in human care do not expend energy in the same manner [41]. Considering the brevity of the activities, fast days, and time when no staff are at the facility [10], it is likely that resting time is similar to or exceeds that of wild lions. Increasing activity levels and decreasing rest time in captive lions through novel enrichment in its many forms, while perhaps not matching the activity budgets of wild lions, compensates for the relative ease of access to food [42].

4.2. Exploration

Under both novel enrichment conditions, subjects spent more time engaging in exploratory behaviours and less time resting, concurrent with previous findings in felids [16–18]. Within the enrichment categories, there were additional differences in the rates of behaviour change; for example, exploration behaviours were recorded more frequently with the sheet enrichment than for the lavender and mirrors strategies. Variability in the extent of behaviour change with different enrichment techniques may be attributed to the fact that the different types of enrichment assessed, while encouraging similar overall benefits, targeted different exploratory behaviours. Mirrors and other visual illusions, for example, encourage the lions to be vigilant and alert [30], while lavender and scent-based enrichments encourage exploration through olfaction [27–29]. The sheet tied to a tree is more manipulative in nature and, while the weather was not recorded, could have been affected by the wind causing extra movement, possibly drawing more attention and eliciting more interaction.

It is important to note that, as with many species, it has been suggested that felids quickly habituate to novel changes in the environment [29]. In typical zoo practice, many different strategies are used to ensure that this is not the case, such as providing intrinsic, exploration-based enrichment on a rotation basis [18] or providing multiple types of enrichment simultaneously [17]. Different types of enrichment, where possible, can be provided within different sensory categories depending on the senses a species is well adapted to utilise. For felids, which have powerful senses of smell, scented enrichment works well [17]. For example, while lavender was new to the lions in this study, other types of scented enrichment, such as herbivore dung, which was used at least once a month, had been used regularly prior. As we did not measure the long-term impacts on behaviour in this study, this topic warrants further examination to understand the specific behavioural responses to sensory enrichment over longer periods. It would also be beneficial to look at other types of sensory enrichment and their effects on lions, such as music, animal sounds, and other types of auditory stimuli, as only a few select stimuli were examined in the present study.

Mellor et al. [43] propose that animals successfully achieving chosen goals, such as exploring, contributes to positive welfare outcomes. They suggest that animals may be motivated to display environment-based exploration behaviours, as satiating curiosity can be rewarding. This sentiment aligns with the 24/7 across lifespan model, which states that the ability to express species-specific natural behaviours conducive to optimising emotional states is a welfare criterion [10]. Thus, providing animals with species-specific scenarios to

explore and manipulate, even in the absence of a food reward, is a vital component of a holistic enrichment programme, allowing zoos to encourage a wide range of behaviours through various forms and presentations of novel items.

4.3. Stereotypic Pacing

Although long-term undesirable stereotyped behaviour is a common concern for large carnivores in zoos [2], this was not the case for the lions at Orana Wildlife Park at the time of study, as a very small percentage of stereotypy was observed. However, the results may still be useful for zoos that struggle with undesirable behaviours in lion prides housed in their facilities.

While there was no significant decrease in the incidence of stereotypic pacing in the lions with the provision of enrichment, it is worth noting that pacing was not observed at all under enrichment conditions, when compared with baseline levels of pacing that were initially already low. When compared with other studies of enrichment in large felids, Orana Wildlife Park's lions had a less than 5% baseline occurrence rate of stereotypic pacing, whereas lions in other studies demonstrated rates as high as 50% of all observations [41]. It is likely that a multitude of factors contributed to the relatively low baseline levels of stereotypy at the outset. The practice of housing two prides in rotation in large enclosures, as opposed to a single pride, is unique to Orana Wildlife Park; single enclosure environments are far more common both in the literature and in accredited zoos. Rotating enclosures have a known behavioural impact on primates [44,45], and it would stand to reason that similar effects would be seen in other territorial species, such as lions. Furthermore, the baseline data of the present study did not completely exclude all enrichment practices which were common aspects of daily management, and no new novel enrichment devices were added on baseline days. Enclosure rotations, visitor encounters, and permanent enclosure design fixtures such as buoys, which were always present in the exhibit and other forms of enrichment, remained normal throughout the study. While the Lion Truck encounter always occurred in the afternoon and thus was never included in the morning's behavioural observation, the levels of enrichment given to the prides as part of their daily routines may have impacted their baseline behaviour overall.

It is also problematic that pacing is defined differentially between studies, which can make comparison of results difficult. For example, while pacing is defined in this article as one back-and-forth loop, other studies may have different definitions; the other definitions provided include uninterrupted repetitive motion along a given route [27] and some studies do not define what was classed as pacing at all [19]. At which point continuous walking becomes classified as pacing in a study, and at what stage it is considered maladaptive, is unclear.

Furthermore, as this study did not examine the long-term effects on the behaviour of different enrichment types, it is unclear whether these strategies have residual benefits in the days or weeks following enrichment. For enrichment to be successful in promoting positive long-term psychological health, stereotyped behaviours indicating lower welfare states should be lower even when the enrichment item is no longer present [18]. Of course, due to the low levels of stereotyped behaviour seen in the study group, enrichment strategies could be consistently provided to maintain positive behavioural outcomes; however, this comes at the risk of the animals becoming [26]. An effective and practical solution to this challenge adopted by many zoos is to rotate enrichment strategies on a regular basis to avoid habituation; indeed, under AZA accreditation standards, a formal enrichment programme, which includes a variable schedule, will promote species-specific behavioural opportunities and aid in the prevention of maladaptive stereotypies [46].

4.4. Social and Territorial

The unique way Orana Wildlife Park housed the lions during this study, and indeed as they continue to do so, must be acknowledged when discussing social behaviour in the study groups. While the prides were not rotated between enclosures for consistency in the results during the study itself, it continued to be part of the daily management procedure to rotate the prides between the two outdoor enclosures. This rotation of exhibits already provides significant enrichment by encouraging naturalistic territorial behaviours, such as the ability to scent mark and scratch in places where another pride has been. To our knowledge, no other studies have been conducted on lions held in a comparable manner, nor are behaviours frequently measured in enrichment studies. Comparing the results of the present study with those of lions held in single-pride scenarios is challenging. Nonetheless, the significant impacts of the different enrichment categories on territorial behaviour warrant discussion.

Overall, the use of non-food-based enrichment was associated with a significant increase in territorial behaviours, such as rubbing and scent-marking. Within these categories, there were further significant effects; providing the lions with eggs led to the most substantial increase in territorial behaviours when compared with the ice blocks and gelatine. Such territorial behaviours in the presence of food are inconsistent with previous findings in lions. For example, in a recent study conducted on lions which were carcass-fed with fast days, feed days were associated with increased marking behaviours [47].

Feeding is highlighted as the most common context for territorial behaviours to occur in lions, both in the wild and in captivity [48]. While the practice of holding two prides likely leads to increased levels of territorial behaviour when compared with a facility with a single-exhibit, single-pride housing system, it is interesting that the presence of food was associated with less territorial behaviour than other types of enrichment and no enrichment types significantly impacted social behaviour within the prides. The increase in alertness associated with the mirrors, as has been observed with other types of optical illusions [30], may be one cause. Lavender enrichment promoted significantly higher levels of territorial behaviours compared with the other non-food enrichment types, and so such behaviour may be a component of the behaviours which lions use to explore unfamiliar scents. It would be beneficial to see how other types of scented enrichment impact territorial behaviours and how this may differ for lions which are not held within a multiple-pride system.

4.5. Limitations

Prior to disseminating the results, the unique housing situation at Orana Wildlife Park and the limitations of the study herald discussion. Housing two prides of lions in a rotation system is uncommon. Therefore, it is difficult to generalise these results to lions maintained in other housing situations. Additionally, enrichment was regularly used for these groups of lions outside the research period and continued to be provided in the form of daily Lion Truck feed throughout the study.

We were also limited by the historic nature of these data, which were collected a decade prior to disseminating these findings; therefore, some information was difficult to obtain, or records no longer existed. For example, information on which pride was being fed versus having a starve day on each day of data collection, despite the understanding that starve days may have an impact on the behaviour of large carnivores [49]. Detailed historical information on the types of novel enrichment that had been attempted before was also unavailable. If the study had been conducted in the present day, more information would have been available, as Orana now maintains more detailed records. Retrospectively, though this information would have been useful, the study was conducted at a time when

such records were not available. Furthermore, best practice for zoos and animal welfare management has progressed in many ways in the ten years since this study was initially conducted, and the management of the lions at Orana has evolved accordingly. These are important considerations when retroactively disseminating the results.

It is also worth mentioning that, while there were three instances of non-food and food enrichment, the specific enrichment used varied, and each individual subtype was only used and measured for one session. This decision was made to reduce the likelihood of anticipation. It is also important to note that ethogram coding may have inflated the time spent in the “explore” category while under-representing “eat” behaviours, especially as food enrichment was provided on three of the six enrichment days. To address this, future studies could benefit from recording food-enrichment observations to distinguish between “explore” and “eat” behaviours related to enrichment. Alternatively, a methodology similar to that of Hamilton et al. [50], wherein interactions with food enrichment are categorised as foraging behaviour, could be employed to clarify insights. If the results were to be repeated in the modern day, there would likely have been multiple repetitions of each enrichment condition to increase the reliability and validity of the data collected. Nonetheless, the data collected provide valuable insight into the impact of different categories of enrichment and different specific enrichment provisions on the behaviour of the Orana Wildlife Park lions.

5. Conclusions

Overall, the results of this study demonstrate how various types of novel enrichments differentially impact the behavioural profile of lions housed within a zoological facility. While most studies and, indeed, the majority of enrichment practically provided to large carnivores in zoos focus on feeding and hunting, these results highlight a number of novel enrichment strategies, both food and non-food, which can be used to encourage naturalistic and rewarding behaviours. It is paramount to continually evaluate the efficacy of many of these techniques and explore the impact of new types of enrichment to ensure that a vast library of techniques is maintained and supported by biological evidence.

The results also suggest that enrichment programmes may consider the nuances of wild-type behaviour when designing and implementing new strategies to maximise the behavioural opportunities offered to animals. Encouraging a variety of different natural behaviours through a large library of enrichment strategies, all carefully evaluated for their effectiveness, contributes to the positive psychological and physical health of animals in human care. Utilising a wide variety of enrichment strategies which aim to encourage different wild-type behaviours in lions should form part of a holistic behavioural management approach which stimulates a more natural and diverse activity budget, where possible preferably focusing on validated animal welfare measures that are sensitive to valence.

Behaviour management, including environmental enrichment, is best approached from a 24/7 across lifespan approach through the lens of the most recent Five Domains model. This study provides valuable information to aid goal-based enrichment programs for lions, utilising a variety of low-cost, accessible, and practical strategies. These findings highlight how novel enrichment items can be used to encourage a wide behavioural repertoire in a social felid. The findings of this study contribute to the growing literature regarding the evaluation of enrichment techniques for zoo-housed carnivores.

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