CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Tropical AgriSciences

The Effects of Olfactory Enrichment and Presentation on Tigers' (*Panthera tigris*) Behaviour

MASTER'S THESIS

Prague 2021

Author: Corrie Elizabeth Rushford

Chief supervisor: Doc. Francisco Ceacero Herrador, Ph.D.

Declaration

I hereby declare that I have done this thesis entitled “The Effects of Olfactory Enrichment and Presentation on Tigers’ (*Panthera tigris*) Behaviour” independently, all texts in this thesis are original, and all the sources have been quoted and acknowledged by means of complete references and according to Citation rules of the FTA.

In Prague 05/08/2021

....

Corrie Elizabeth Rushford

Acknowledgements

I would like to thank the following people and organizations for their support, time, encouragement, and everything in between that helped make this project possible.

First, I would like to thank my thesis advisor, Professor Francisco Ceacero Herrador PhD., for all his support and patience in choosing a topic, flexibility with topic changes, providing contact with the Prague Zoo, as well as with advice and assistance in the data analysis and technical writing aspects of this thesis.

Secondly, I would like to thank The Prague Zoo for giving me the opportunity to conduct this thesis research within their facilities and for providing the materials for the enrichment. Specifically, I would like to give thanks to Marketa Lavicka, who was my primary contact at the Prague Zoo and was a great help in facilitating the data collection, organizing the enrichment schedule, and providing information and insight on tiger enrichment.

Finally, I would like to thank my friends and family for their continuous support of my decision to further my education abroad. I cannot thank my mother, Christie Rushford, and my grandmother, Arlene Carpenter, enough for emotional support throughout my master's studies; this project would not have been possible without it. To my friends and classmates, thank you for your words of encouragement, constructive comments, and ever helpful proofreading assistance.

Abstract

With more tigers in captivity within The United States alone than in the wild, zoos' role in tiger (*Panthera tigris*) conservation has become increasingly important (World Wildlife Fund). Zoos should have high health and welfare standards, but felines are challenging in captivity as they frequently exhibit agonistic and stereotypic behaviours (Clubb et al. 2003). As tigers are both a flagship species and Endangered in the wild, zoos should always make sure to prioritize their health, one way to do this is by including enrichment in their enclosures, and this study evaluated the effects of various olfactory enrichment and their presentation (Clubb & Mason 2007; Maple & Perdue 2013). This study used four enrichment scents, two of which were animal-based (conspecific and fish oil) and two plant-based (catnip and rosewater). These scents were presented on boxes, wicker balls, or rubbed in the enclosure to determine if the enrichment presentation played a significant role in its success. This study found that overall olfactory enrichment led to higher levels of inactive behaviour, but stereotypic behaviour was lower during the enrichment than before or after the enrichment period. The increased inactive behaviour may be due to the enrichment timing or to each individual's personal preference. Some individuals' cautious approach and interaction with the enrichment objects may reflect their reaction in the wild to novel stimuli. However, further study is needed to determine if it is beneficial to tigers in captivity. Visitors feel more connected to nature and are more willing to contribute to conservation projects when they have positive zoo encounters, specifically with flagship species. The second purpose of this study aimed to establish if offering olfactory enrichment affected tigers' behaviour in such a way that visitor engagement and length of the visit were also affected. This study found that visitor engagement and visit length reflected tigers' activity level and visibility. Considering that zoos play a critical role as ambassadors between wildlife and humans, zoos should consider visitors' perceptions when designing enclosures and enrichment regimes (Gusset & Dick 2011).

Key words: Felid, Animal Behaviour, Zoo, Enrichment Tools, Captivity, Welfare

Contents

List of tables

List of figures

List of the abbreviations used in the thesis

AWPIS© = Animal Welfare Priority Identification System

CR = Corrie Rushford

IUCN = International Union for Conservation of Nature and Natural Resources

1. Introduction and Literature Review

1.1. Tigers' Ecology and Behaviour in the Wild

Tigers (*Panthera tigris*) are an iconic large felid species, with nine subspecies, native to southeast Asia, the Himalayas, India, China, and Russia. Although they primarily inhabit tropical forests, their range used to be much more extensive and included dryer and colder climates. In China and Russia, tigers inhabit habitats from sea level up to 4,500 meters above sea level (Goodrich et al. 2015). In the wild, adult tigers can have home ranges up to 1000 square kilometres depending on prey availability and the region (Breton & Barrot 2014). An adult tiger can, on average, travel 32 kilometres in a day, and males tend to travel further than females (Dacres 2007). Like other felid species, tigers are predominantly solitary but exhibit the typical feline social pattern where an adult male's home range overlaps between 1-3 females' ranges (Goodrich et al. 2015). Tigers' movement and territories reflect their main prey species, such as boar and deer (Hayward et al. 2012; Breton & Barrot 2014). Although not their preferred prey species, tigers may hunt much smaller and larger prey, such as junglefowl and moose, as necessary (Hayward et al. 2012). It is not typical for wild tigers to eat every day, and they can fast for up to four days in a row without affecting their fitness (Dacres 2007). Human activities such as development, agriculture, hunting, and trapping are the primary threats to wild tiger populations. Tigers are listed as an endangered species by the International Union for Conservation of Nature and Natural Resources' (IUCN) red list (Goodrich et al. 2015). According to the World Wildlife Fund, about 5,000 tigers live in captivity in the United States alone, whereas the wild population is only estimated to be about 3,200 individuals (World Wildlife Fund). As more tigers live in captivity than in the wild, zoos play a crucial role in conserving the species.

1.1.1. Olfaction in Felids

All vertebrate species use their sense of smell to monitor their environment to some degree, and according to Sommerville and Broom (1998), have some level of olfactory awareness. Different scents can elicit various responses; particularly in felids, they can elicit scent rubbing, rolling, or flehmen (Reiger 1979). Scent rubbing is when an individual extends its neck and rubs it against an object. Felids prefer to mark with their cheeks, including chin, neck, shoulders, and back (Reiger 1979). Of the five odours Reiger (1979) investigated, food, chemicals, catnip, urine, faeces, and conspecific scent mark, tigers only scent rubbed in reaction to urine, faeces, and conspecific scent marks. Rolling is less common but elicited by strong scents (Reiger 1979). Flehmen occurs after smelling, and the individual pulls back their lips into a grimace, and their mouth hangs open a little. This action moves the odour to Jacobson's organ (Sommerville & Broom 1998). The Jacobson's organ is a cluster of sensory cells located in the main nasal chamber that is very important to chemical communication, for example, when an individual is in oestrus (Zug). A study by Cederlund (2018) only recorded a flehmens response to conspecific odours.

Contrary to common belief, tigers do not heavily rely on their sense of smell for hunting, nor do they scent-mark in response to scents of excrement and urine of prey animals (Reiger 1979; Sea World). Tigers have a small number of olfactory cells in their nose, generally used for intraspecies communication (Sea World). When felids scent mark, they leave information about an individual's age, sex, health, reproductive status, and genetic status (Soso et al. 2014). Thus, both urine and faeces are commonly used by felids to mark territories and to attract non-related conspecifics for mating. Since felids are generally solitary, olfaction is especially relied upon for reproduction (Sommerville & Broom 1998).

1.2. Captive Tiger Behaviour

Tigers are held in facilities, such as zoos, for various reasons, including education, recreation, conservation, and research (Gnomes et al. 2019). One problem that all animals face in captivity is that all "essential requirements for survival," such as food, shelter, and water, are provided by their caretakers (Veasey et al. 1996). The void created by not needing to search for essential survival requirements and the facilities' environment can affect tigers' behaviour, sometimes leading to more lethargic, stereotypic, and agonistic behaviours (Veasey et al. 1996; Carlstead & Shepherdson 2000). Stereotypic behaviour is any abnormal and repetitive behaviour not commonly displayed in the wild, for example, pacing, head bobbing, and bar biting (Furlong et al. 2021). Agonistic behaviours are any social behaviours related to aggression, such as circling, chasing, injuring, and threatening another conspecific (Höttges et al. 2019). As shown in a study by Li-wei et al. (2002), tigers in captivity spent most of the day sleeping (52.98%), followed by resting (22.05%), moving (19.57%), and eating (2.27%). In a multi-facility study by Clubb and Mason (2007), 16.43% of tigers' observations were stereotypical behaviours. When the environment is sufficiently stimulating and naturalistic, playful and, natural behaviours are more common than agonistic or stereotypical behaviours (Clayton & Shrock 2020).

1.3. Stressors in Modern Zoos

In captivity, a tiger's environment is drastically different from that of a wild tiger. This difference is likely stressful for the captive individual. Captive tiger's environmental stressors could include small enclosure size compared to natural home ranges, diurnal activity patterns instead of nocturnal, a prepared diet rather than live prey, the inability to hide, strong olfactory and auditory cues, as well as the proximity to other tigers, felid species and humans (Carlstead & Shepherdson 2000; Szokalski et al. 2012). These stressors are often chronic and can cause individuals to exhibit agonistic and stereotypic behaviour such as pacing, chasing, or fighting, and it can also cause health problems such as gastroenteritis (Carlstead & Shepherdson 2000).

Tigers' enclosure size varies significantly among zoos, but all enclosures are much smaller than a tigers' average home range (Breton & Barrot 2014). The study by Breton and Barrot assessed how enclosure size affected 38 tigers' pacing behaviour and determined that larger exhibits lowered the time the individual spent pacing. Another study by Clubb and Mason (2007) compared 33 carnivore species and found species with more extensive natural home ranges and extensive daily travel distances have a higher probability of displaying stereotypic behaviour in captivity. Their study also suggested that removing the decision-making factor of traveling far distances plays a role in exhibiting stereotypic behaviours, but further research is needed to confirm this hypothesis (Clubb & Mason 2007). A recent study by Veasey (2020) conducted an Animal Welfare Priority Identification System (AWPIS©) ranking for Amur tigers, which concluded that the top psychological priority was foraging followed by survival behaviours, active behaviours, and choice decision making. Veasey (2020) expanded on the previously discussed studies by stating that stereotypic behaviours may not be a consequence of the reduction of habitat size but also of reduction in cognitive opportunities.

Another feature that differs across zoos' enclosures is how naturalistic and enriched the spaces are. A housing study by Moreira et al. (2007) examined how moving an individual from an enriched enclosure to a sterile and unenriched enclosure increased the levels of stress hormones produced. This contradicts a study by Sajjad et al. (2011), which showed lower levels of stereotypic behaviour and resting in enriched housing but with similarly elevated levels of stress hormones. According to a previous study, a more complex enclosure, or one with more barriers available to hide behind, decreased the time spent pacing in small cats (Mellen & Shepherdson 1997).

In most zoos, tigers are either housed solitarily (with conspecifics nearby) or in pairs. According to De Rouck et al. (2005), tigers housed with conspecifics in adjoining enclosures exhibited higher levels of pacing. Another study focusing on small felids showed that when housed in groups larger than two, the individuals were less likely to reproduce and exhibited higher levels of pacing when compared to felids housed in pairs (Mellen & Shepherson 1997). De Rouck et al. (2005) concluded that, although wild tigers tend to be solitary, housing a pair of tigers in the same enclosure is preferable. Overall, it is thought that species with large home ranges, such as felids and other carnivores, have a hard time adjusting to living in captivity (Clubb et al. 2003).

1.4. Environmental Enrichment

Many of the problems captive animals exhibit in zoos may be due to stress caused by the differences in their environment between captivity and the wild (Tennessen 1989). Although environmental enrichment has a long history stretching back to 1925, it has not been commonly used until more recently (Mellen & Shepherdson 1997). According to Maple and Perdue (2013), enrichment was initially used as a "posthoc effort" to decrease undesirable behaviours in captive animals. Present-day zookeepers use environmental enrichment as a proactive measure to help improve captive animals' physiological and psychological health by increasing natural species-specific behaviours (Clubb & Mason 2007; Maple & Perdue 2013). Unfortunately, enrichment does not entirely eradicate stereotypic behaviours; it only reduces them (Clubb & Mason 2007). In other cases, individuals exhibit a "behavioural scar," when stereotypy persists after an individual switches from a sterile environment to a sufficiently enriched enclosure (Mason 2006). Some examples of enrichment would include enclosures designed to look similar to the natural habitat of its inhabitants, objects placed in the enclosures aimed to trigger specific behaviours, and exposure to conspecifics or other species. There are various types of enrichment that keepers can use in the enclosure, and they must choose the best option for the species based on the type of behaviour they wish the individuals to exhibit. Keepers must also consider the presentation of the enrichment as it will affect how the individual interacts and responds to the enrichment (Tarou & Bashaw 2006). According to Maple & Perdue (2013), enrichment falls into nine categories: feeding, tactile, structural, auditory, olfactory, visual, social, human-animal, and cognitive.

An individual's interaction with enrichment devices is motivated by two types of reinforcement, extrinsic and intrinsic. Intrinsic reinforcement is when an individual will repeat a behaviour due to internal motivation (Tarou & Bashaw 2006). Examples of enrichment that uses intrinsic reinforcement would be exposure to a new enclosure, olfactory stimulus, or exposure to a conspecific or another species. In comparison, extrinsic reinforcement occurs when an individual performs a behaviour due to an external reward, such as food or nesting material (Tarou & Bashaw 2006). According to Tarou and Bashaw (2006), enrichment that provides extrinsic reinforcement generally has longer-lasting effects when compared to intrinsic reinforcement. However, both intrinsic and extrinsic reinforcement have the possibility of habituation or the loss of interest in an object over time. Habituation to the enrichment item can occur within, during the same enrichment session, or across multiple sessions (Tarou & Bashaw 2006). Spontaneous recovery, the reappearance of a reaction to a previously habituated enrichment, can occur if the enrichment device is not used for a period of time (Tarou & Bashaw 2006). Clayton and Shrock (2020) concluded that some of the tigers in their study responded to the enrichment item due to its novelty rather than the tigers' preference. Thus, using many forms of enrichment, utilizing both intrinsic and extrinsic reinforcement, on a rotation can help slow habituation to enrichment items (Tarou & Bashaw 2006).

According to Podturkin and Papaeva (2020), the natural behaviours commonly targeted in felids include exploring, flehmen, sniffing, dragging, and pulling objects. Enrichment items previously used in tiger enrichment studies include barrels, boxes, olfactory simulations, and feeding poles. Although many of them are widely used, not all forms of enrichment have been closely studied to determine their benefit to the individuals and species (Saskia et al. 2002; Gardiánová et al. 2014; Gomes et al. 2019). A master's thesis study by Pitsko (2003), showed that tigers' stereotypic behaviours decreased, and their exploratory behaviours increased with more natural enclosures containing various substrates, foliage, and enrichment items. Presenting only one enrichment item may not be sufficient to change behaviour; Clayton and Shrock (2020) stated that determining individuals' enrichment preferences is essential for evaluating environmental enrichment strategies because preferred items are more effective in promoting targeted behaviours. A study by Schmidt (2012), observed two ocelots' (*Leopardus pardalis*) reactions to various types of enrichment and concluded that keepers could better understand each animal's behaviour through environmental enrichment.

1.4.1. Olfactory Enrichment

Wild tigers utilize olfactory signals for intraspecies communication and are essential stimuli (Wells et al. 2017). In captivity, enclosures lack these olfactory changes, and cleaning agents' smell replaces more natural scents (Szokalski et al. 2012). Zookeepers have started using different scents to help promote more exploratory behaviours, and previous studies have specifically looked at the effects of spices (Skibiel et al. 2007; Damasceno et al. 2017), zebra dung as well as scented squash (Van Metter et al. 2008). They found that olfactory enrichment increases active behaviours such as running, walking, jumping, climbing, swimming, sniffing objects, flehmen, stretching, and sharpening claws (Szokalski et al. 2012). A study conducted by Rosandher (2005) showed that when given a choice, snow leopards interacted more frequently with an odorized enrichment object over a non-odorized of the same type and that both odour and the presentation changed snow leopard behaviour. The behavioural response to olfactory enrichment is motivated by intrinsic reinforcement, and this produces high response levels on the first day of presentation but a significantly lower response on the second day (Tarou & Bashaw 2006). A recent study by Clayton and Shrock (2020) determined that some of the tigers in their study have scent preference, between unscented, Calvin Klein Obsession and cinnamon, while others did not. They concluded that rotating between scented and unscented enrichment objects could add different variations without largely increasing the budget. Similarly, Mellen and Shepardson (1997) stated that it is critical to vary the location of enrichment objects, scents, and olfactory enrichment frequency as felids habituate quickly to enrichment objects. Olfactory enrichment may be a way to replicate the cognitive aspects of feeding and foraging behaviours in the wild. (Veasey 2020).

1.5. Visitors Perspective

Zoos have a long history tracing back to ancient times; one of the first recorded zoos was in Hierakonpolis, Egypt (Boissoneault 2015). Unlike most modern zoos, a variety of animal species were kept together in a large enclosure (Boissoneault 2015). Early zoos acted as a "museum" of animals, where the individuals were kept in small, bare, and sterile cages with a viewing area for visitors to see through (Rutledge et al. 2011). Today, zoos not only entertain and educate guests, but many have conservation and research goals. In both urban and suburban zoos, there has been a shift to more natural and enriched enclosures; brought about by activists who argued for the welfare of the animals (Rutledge et al. 2011). Davey et al. (2005) demonstrated that an environmentally enriched enclosure attracted more zoo visitors, and the visitors spent more time observing than at sterile enclosures.

According to Powell and Bullock (2014) and Consorte-McCrea et al. (2019), visitors who experienced more positive emotions while visiting a zoo also report higher respect for nature and are more willing to participate in conservation efforts. Many factors influenced these positive emotions, including whether the visitor felt they had an "encounter" with the animal and if the visitors had a vivid experience (Consorte-McCrea et al. 2019; Powell & Bullock 2014). As stated previously, one of the goals of environmental enrichment is to promote species-specific behaviours such as exploration (Podturkin & Papaeva 2020). Environmental enrichment promoted stronger "encounter" responses in visitors and scored higher in positive attitudes on surveys when the animals exhibited increased species-specific and active behaviours (Powell & Bullock 2014; Salas et al. 2021). In a study by Salas et al. (2021), visitors scored enclosures with enrichment objects higher in enclosure suitability. When an animal exhibits stereotypy and abnormal, repetitive behaviours, it is commonly perceived negatively by the public (Clubb & Mason 2007; Miller 2012; Godinez et al. 2013; Salas et al. 2021). Thus, not only does an enrichment environment promote healthier behaviour in tigers, visitors are happier when zoos offer more stimulation to the animals (Powell & Bullock 2014). This connection is critical considering, globally, around 700 million people visit zoos annually. Zoos now play critical roles as ambassadors between wildlife and humans (Gusset & Dick 2011).

As zoos lead to a stronger connection with nature, they also help reduce fear of wildlife and address human-wildlife conflicts (Consorte-McCrea et al. 2019). Visitors are particularly emotionally affected by more attractive species such as tigers than other less desirable species such as the hyena (Hyaenidae sp.) (Powell & Bullock 2014). Using their charisma, tigers and other popular large carnivores act as “ambassador species” for other species. The protection of ambassador species’ large home ranges creates an umbrella effect that benefits biodiversity conservation (Consorte-McCrea et al. 2019). Since zoos act as a bridge for visitors to observe elusive and rare species and promote conservation efforts, zoos must take visitor perspectives into account when designing and enriching animal enclosures.

2. Aims of the Thesis

Carnivores, particularly those with large home ranges, are among the most challenging groups of animals to maintain mentally and physically healthy in captivity (Kroshko et al. 2016). Skibiel et al. (2007), Van Metter et al. (2008), and Damasceno et al. (2017), among others, have shown that olfactory enrichment is beneficial to tigers. However, these studies did not assess various scents and their presentation or the difference between animal-based (conspecific and fish oil) and plant-based (catnip and rosewater) enrichment. A small section of this study assessed the visitors' time spent at the enclosure and the level of engagement with the tigers. Through the four aims listed below, this study will aid in a better understanding of tigers' responses to olfactory enrichment, helping to facilitate improved lives for captive tigers. By aligning tigers' activity profile with their wild counterparts, stereotypical and agonistic behaviours should decline, resulting in physically and psychologically healthier individuals.

1. Compare behaviour profile with and without the use of the olfactory enrichment.
2. Determine if there is a difference between animal-based (fish oil and conspecific) and plant-based (rosewater and catnip) olfactory enrichment.
3. Establish if the presentation of the enrichment (boxes, wicker or rubbed in the enclosure) makes a difference in the time spent interacting with the enrichment.
4. Assess visitors' engagement and length of stay with and without tigers' presence and activity.

3. Methods

3.1. The Prague Zoo

The Prague Zoo opened its doors on September 28, 1931, and is part of the European Association of Zoos and Aquariums. It was initially home to only a few species, including a wolf, Przewalski's horses, tigers, an elephant, a hippopotamus, and a rhinoceros. As of 2018, the Prague Zoo has a total area of 58 hectares and 676 species, of which 563 are listed as endangered by the IUCN red list. It currently welcomes about 1.4 million visitors each year, and according to Tripadvisor, it is the second most visited attraction in Prague, just behind Prague Castle. In 2015 The Prague Zoo was ranked as the 4th best zoo in the world, and in 2020 it received the Travelers Choice Award from Tripadvisor. The Prague Zoo is actively involved in various conservation projects worldwide, including reintroducing Przewalski's horses in Mongolia and bearded vultures in the Czech Republic and monitoring gharials and their habitat in India (Prague Zoo).

3.1.1. Prague Zoo Tigers

The Prague Zoo is home to three subspecies of tiger, including Malayan tigers (*Panthera tigris jacksonii*), Sumatran tigers (*Panthera tigris sumatrae*), and Siberian tigers (*Panthera tigris altaica*). Each sub-species has one male and one female who are either kept together in the enclosure or kept separately by being rotated between the indoor and outdoor enclosure. All three sub-species are fed on a high-frequency diet consisting of 4 kilograms of meat on the bone, with fasting days on Thursdays and Sundays. Due to time constraints, this study only focused on the Malayan and Sumatran tigers.

3.1.1.1. Malayan Tigers (*Panthera tigris jacksonii*)

Banya is the female Malayan tiger (Figure 1); she was born on April, 21st 2006, and was fifteen years old at the time of this study. Johann is the male Malayan tiger (Figure 1); he was born on February 10th, 2007, and was thirteen years old at the time of this study. The Malayan tigers' enclosure also includes a feeding pole used for enrichment. Although the Malayan tigers share an enclosure, they are a mating pair and are kept separate, so during this enrichment assessment, only the male interacted with the enrichment object.

Figure 1: Banya (left) and Johann (right). Credit: CR, 2020.

3.1.1.2. Sumatran Tigers (*Panthera tigris sumatrae*)

Cinta (Figure 2) is the youngest of the tigers at seven years old during this study. She was born on February 3rd, 2014. Falco is the male Sumatran tiger (Figure 2); he was born on May 27th, 2007, and was thirteen years old at the time of this study.

Figure 2: Cinta (left) and Falco (right). Credit: CR, 2020.

3.1.2. Enclosures

Enclosure design influences tigers' behaviour, where more naturalistic and enclosures further away from anthropogenic sounds lead to less stereotypic and agonistic behaviours (Gnomes et al. 2019; Pistsko 2003). At the Prague Zoo, the two enclosures in this study are located side by side, and both include an outdoor area and an indoor area

(Figure 3). Part of the indoor area is away from visitor sight, and in the other part, the visitors can see the tigers. Both indoor areas are primarily concrete with metal bars and have little or no natural aspects. The enclosures' outdoor areas include a large swimming area, a grassy area, a two-tiered raised platform, logs, shrubs, rocks, and trees as seen in Figure 4 and Figure 5 below. The two outdoor areas align with the essential aspects of tigers' enclosures as described by Pistsko (2003); each enclosure is comprised of enough space for the individuals to run and explore, natural vegetation, high shaded places, and a body of water.

Figure 3: Malayan enclosure (left) and Sumatran enclosure (right) Credit: Google maps, 2021.

Figure 4: Outdoor Malayan Tiger Enclosure. Credit: CR, 2020.

Figure 5: Outdoor Sumatran Tiger Enclosure. Credit: CR, 2020.

3.2. Enrichment Assessment

To compare the tigers' behaviour al profile before, during, and after olfactory enrichment, this study focused on two of the three subspecies of tigers at the Prague Zoo, the Malayan tigers and the Sumatran tigers. First, the tigers' baseline behaviour was monitored for five days in the absence of any olfactory enrichment. The days and times were chosen randomly by assigning flipping a coin to determine if the day in question will be monitored, assigning numbers to the time frames, and rolling a dice to determine what time would be monitored. All behaviour al observations were recorded for three hours, five days of the week. All data was collected between June 2020 and August 2020.

After the baseline data was collected, the enrichment assessment began. As suggested by the enrichment coordinator at the Prague Zoo, enrichment days were alternated between the two sub-species to ensure that the previous odor was mostly dissipated. The enrichment coordinator chose which items and odors were offered each enrichment session and tried to alternate between the different options. The enrichment items were placed in an open area of the outdoor enclosure during enrichment days, which could be easily seen from the visitors' area, around 14.00h. Two of each enrichment option were presented, one sprayed with the enrichment scent and the other without.

Tigers' behaviour was monitored using continuous sampling day of enrichment and the day after the enrichment. The second day was used to determine if the individuals' behaviour change continued through the second day. Each time the tigers interacted with one of the enrichment objects, it was noted how they manipulated the object. Behaviours were categorized using table 1 below.

Table 1: Ethogram of tiger behaviours recorded before, during and after the presentation of olfactory enrichment in the Prague Zoo facilities

Main Behaviour	Agonistic	Stereotypic	Feeding	Inactive	Social	Active	Out of Sight
Sub-Behaviour	Fighting Chasing Threaten	Pacing Circling Bar-biting Head-Bobbing	Hunting Eating Drinking	Sleeping Resting Sitting Grooming	Playing Nuzzle Allogrooming Mounting Marking Calling	Walking Playing Exploring Sniffing	Out of Sight

Aligning with previous felid enrichment studies, three main behaviour groups were focused on comparing the tigers' behavioural profile before, during, and after olfactory enrichment (Clayton and Shrock 2020; Damasceno et al. 2017; Höttges et al. 2019; Mason & Rushen 2006; Schmidt 2012; Skibiel et al. 2007; Rosandher 2005; Van Metter et al. 2008). These three behaviours were chosen because, generally, enrichment aims to decrease stereotypic and agonistic behaviour and increase active behaviours (Clubb & Mason 2007).

3.3. Odours

Four odours were chosen; two plant-based, catnip and rosewater, and two animal-based, fish oil and conspecific. The conspecific enrichment was placed in the Siberian tigers' enclosure, located on the other side of the Prague Zoo, before being placed in the Malayan tigers' or the Sumatran tigers' enclosure. Each of the four scents was tested and presented on various enrichment objects, as discussed in the following section. Two of the same enrichment items were presented at the same time, one with the olfactory enrichment and one without. This was used to determine if the presentation or the olfactory enrichment triggered a stronger reaction. While the tigers' behaviour was being monitored, the time and frequency the individual interacted with the scented and unscented enrichment item was recorded.

3.4. Presentation

Each presentation option (wicker ball, cardboard box, spread on ground) was used at least once examples of the presentations can be seen in Figure 6 & Figure 7). When the individual approached the object, the approach time stopped upon contact with the object, and the total interaction time was recorded. If the individual did not approach or stopped interacting with the object, the time stopped after 10 minutes of inactivity.

Figure 6: Fish oil Enrichment Displayed on a Box. Credit: CR, 2020.

Figure 7: Catnip Enrichment Displayed on a Ball. Credit: CR, 2020.

3.5. Visitor Assessment

According to Powell and Bullock (2014), animals that are visually appealing to visitors elicit a higher emotional response. In their assessment of visitors' reactions to three carnivorans, tigers elicited the highest emotional response. To determine if olfactory enrichment caused a change in visitors' behaviour, their engagement and length of stay were rated when the enrichment was and was not presented. As visitors approached the tigers' enclosure, the length of time they stayed in front of the enclosure was rated on a scale from 1-5, defined as follows: 1 = 0-1 minutes; 2 = 1-2 minutes; 3 = 2-5 minutes; 4 = 5-10 minutes; 5 = more than 10 minutes. The visitors' engagement in the tigers' activity and the informational signs provided by the zoo was also rated on a scale of 1-5, 1 was very low interest and when people did not look into enclosure; 2 included low interest in animal, brief look into enclosure; 3 was defined as some interest in animal, such as photographs; 4 included medium high animal engagement and photographs, but no sign reading nor discussion; 5 being high engagement, photos, reading informational signs, watching and discussing the animals. During peak visiting hours, every third visitor group seen arriving was selected.

Statistical Analysis

The raw data collected from the tiger behaviour al assessment was first compiled into an excel datasheet. The duration of the observations was calculated by subtracting the start time or the enrichment time from the end time and this number was then converted to seconds. The duration of each sub-behaviour was calculated by counting the difference in seconds between each behaviour. Then the sub-behaviours were grouped into the behaviour groups active, inactive, stereotypic, agonistic, social, feeding, other, and out of sight, as shown previously in table 1. Banya's data from the during phase was marked as not valid, as she never interacted with the enrichment on the first day. The duration of each behaviour group was then added up and condensed into one line per tiger per day, in total there was a sample size of 50 entries between the four tiger individuals. If the approach time was greater than 10 minutes then it was marked as null. Finally, the duration of enrichment interaction was also added together per day per tiger individual. This small sample size did not permit for multivariate analyses, so univariate analyses based on Kruskal-Wallis tests were conducted.

The visitor data did not need to be greatly manipulated from its raw data form. This data was compiled into an excel database and was ready for further analyses. The sample size for the visitor analysis was 3976 entries. Generalized Linear Models were conducted in order to determine the effects of group size, enrichment timeframe, tiger visibility, tiger activity, on length of the visit and engagement by visitors.

4. Results

Shappiro-Wilks was used to test for normality, showing that most of the variables used in the following analyses on tigers´ behaviour do not have a normal distribution. Thus, a non-parametric test was used.

4.1. Enrichment Assessment

The first aim of this thesis is to compare behaviour profile with and without the use of the olfactory enrichment. To determine if the enrichment changed the levels of agonistic, stereotypic, inactive and active behaviours an Independent-Samples Kruskal-Wallis Test was run. The results are shown in Table 2.

Table 2: The Effect of Study Timeframe on Targeted Tigers' Behaviour

	Before (sec)	During (sec)	After (sec)	KW	P-value
Agonistic	49.0	3.6	1.3	0.679	0.712
Stereotypic	402.0	100.2	379.7	4.353	0.113
Inactive	3,360.0	5,742.9	6,144.5	11.274	0.004
Active	835.5	414.8	461.3	4.203	0.122

The results for agonistic, stereotypic and active were not significant. Although there was no significant change in stereotypic behaviour it was higher before and after the enrichment. Active behaviour also did not significantly change but the tigers were more active before the enrichment treatment. Inactive behaviour was displayed at a significantly higher rate during and after enrichment treatment.

An Independent-Samples Kruskal-Wallis Test was also used to determine if there was a difference in behaviour during the enrichment treatment between individuals (Table 3). Similarly, Independent-Samples Kruskal-Wallis Test was run to determine if there was a significant difference in individual approach time and interaction time between individuals.

Table 3: Individual's Behaviour During the Olfactory Enrichment Phase

	Johann (sec)	Falco (sec)	Cinta (sec)	KW	P-value
Stereotypic	118.0	160.6	28.8	3.073	0.381
Inactive	5,815.0	5,736.3	5,704.4	1.007	0.800
Active	339.0	314.4	562.5	1.297	0.730
Average Approach Time (sec)	220.0	126.6	555.0	6.888	0.032
Average Interaction Time (sec)	26.0	11.3	4.3	4.992	0.082

The studied animals did not show any significant difference in stereotypic, inactive and active behaviour during the enrichment treatment. However, there was a significant in the average time it took for the individual tigers to approach the enrichment item. Falco and Johann approached the item much more quickly than Cinta did. Although there was just a marginal significant difference in the time spent interacting with the enrichment items, Johann had the longest interaction while Cinta had the shortest.

4.2. Odours' Effect

The second aim of this thesis was to establish if there is a difference between animal-based and plant-based olfactory enrichment. First, to determine if the specific type of olfactory enrichment had any effect on tiger behaviour an Independent-Samples Kruskal-Wallis Test was conducted. The results are shown in Table 4 below.

Table 4: The Effects of Olfactory Enrichment on Tigers' Behaviour

	Before (sec)	Fish oil (sec)	Conspecific (sec)	Rosewater (sec)	Catnip (sec)	KW	P-value
Agonistic	49.0	0.0	0.0	0.6	10.0	1.566	0.815
Stereotypic	402.0	55.8	210.0	75.0	167.1	3.432	0.488
Inactive	3,360.0	5,945.0	6,537.5	4,911.9	6,519.3	11.082	0.026
Active	835.5	380.8	347.5	290.6	585.7	5.354	0.253

The results for the effects of enrichment type on agonistic, stereotypic and active behaviour were not significant. Although there is no significant difference, stereotypic behaviour was lower during the fish oil and rosewater treatments. However, there was a statistically significant decrease in inactive behaviour before the enrichment period.

To compare the effects of animal-based odours and plant-based odours an Independent-Samples Kruskal-Wallis (Table 5).

Table 5: Comparison of Animal and Plant-Based Enrichment Odours on Tigers' Behaviour

	Before (sec)	Animal-Based	Plant-Based	KW	Significance
Agonistic	49.0	0.0	5.8	0.528	0.768
Stereotypic	402.0	94.4	103.8	2.676	0.262
Inactive	3,360.0	6,093.1	5,527.3	9.024	0.011
Active	835.5	372.5	440.8	3.871	0.144

The results for the effects of animal-based or plant-based enrichment type on agonistic, stereotypic and active behaviour were not significant. Although it was not significant, animal-based and plant-based enrichment tended to have lower stereotypic behaviour than before the enrichment. Inactive behaviour was significantly lower before enrichment than during either the animal or plant-based enrichment treatments.

An Independent-Samples Kruskal-Wallis Test was run to determine if there was a significant difference in average time to approach and interaction time across olfactory enrichment types. The results from this test are shown in Table 6 below.

Table 6: The Effects of Enrichment Type on Approach and Interaction Time

	Fish oil	Conspecific	Rosewater	Catnip	KW	P-value
Average Time to Approach (sec)	303.7	120.0	103.3	165.0	1.069	0.784
Average Interaction Time (sec)	17.5	7.5	11.6	10.0	0.487	0.922

Although the results were not significant the enrichment odour with the fastest average approach time was rosewater and the slowest was fish oil. Interaction time also was not significantly different between the enrichment types. The longest average interaction time was with fish oil and the lowest was conspecific odour. Overall, the longest recorded interaction event was with fish oil and the shortest event was with the conspecific odour.

4.3. Effects of Enrichment Presentation

The third aim was to establish if the presentation of the enrichment (boxes, wicker or rubbed in the enclosure) makes a difference in the time spent interacting with the enrichment. An Independent-Samples Kruskal-Wallis Test was conducted to determine if the enrichment display type affected the tigers' behaviour (Table 7).

Table 7: The Effects of Enrichment Presentation on Targeted Tigers' Behaviour

	Before (sec)	Ball (sec)	Box (sec)	Ground (sec)	KW	Significance
Agonistic	49.0	0.0	7.5	0.0	3.244	0.355
Stereotypic	402.0	0.0	116.5	104.4	4.392	0.222
Inactive	3,360.0	6,780.0	5,507.5	5,773.9	8.159	0.043
Active	835.5	270.0	553.5	292.8	9.354	0.025

The results for the effects of display type on agonistic and stereotypic behaviour were not significant. Whereas the display type had a significant effect on inactive and active behaviours. Tigers were more inactive with enrichment displayed on a ball. They exhibited higher active behaviours with the box and ground enrichment presentation.

An Independent-Samples Kruskal-Wallis Test was run to determine if there was a significant difference in average time to approach across the enrichment display types, the results are displayed below (Table 8).

Table 8: The Effects of the Enrichment Display on Approach and Interaction Time

	Box	Wicker Ball	Ground	KW	P-value
Average Time to Approach (sec)	80.0	300.0	318.7	2.380	0.304
Average Interaction Time (sec)	15.5	7.5	10.5	1.252	0.535

The results from the approach time were not statistically significant but the fastest was the box and the slowest was the ground. The interaction time also was not significantly different between the enrichment display types. The longest interaction time was with the box and the shortest was the ground.

4.4. Visitor Assessment

The last aim of this thesis was to assess visitors' engagement and length of stay with and without tigers' presence and activity. A Kolmogorov-Smirnov tests were run determining normality. Both variables length of the visit and engagement showed not normal distribution, with the histogram revealing a Poisson distribution. Thus, to determine the effect of the group size, presence and activity of the tigers, weather and the timeframe has on the length and engagement of each visitor group, two Generalized Linear Mixed Models were run. As seen in Table 9 the time each group spent at the enclosure increased with the number of adults, the number of children, presence and activity of the tigers, but there was no effect of weather nor of the timeframe. Figure 8 shows the significant difference in visitors' length of visit while the tigers were active or visible.

Table 9: The Effects of Group Size, Tiger Visibility, Tiger Activity and Timeframe on Visitors' Length of Visit

	Coefficient	Standard Error	P-value	95% Upper	95% Lower
Number of Adults	0.034	0.016	0.039	0.066	0.002
Number of Kids	0.029	0.012	0.016	0.053	0.005
Tigers Visible	0.466	0.035	<0.001	0.396	0.535
Tigers Active	0.304	0.036	<0.001	0.232	0.376
Timeframe[1]					
Before-During	0.044	0.042	0.296	0.126	-0.038
Before-After	0.117	0.044	0.007	0.203	0.031
During-After	0.074	0.029	0.010	0.130	0.017

[1] Second one as a reference category

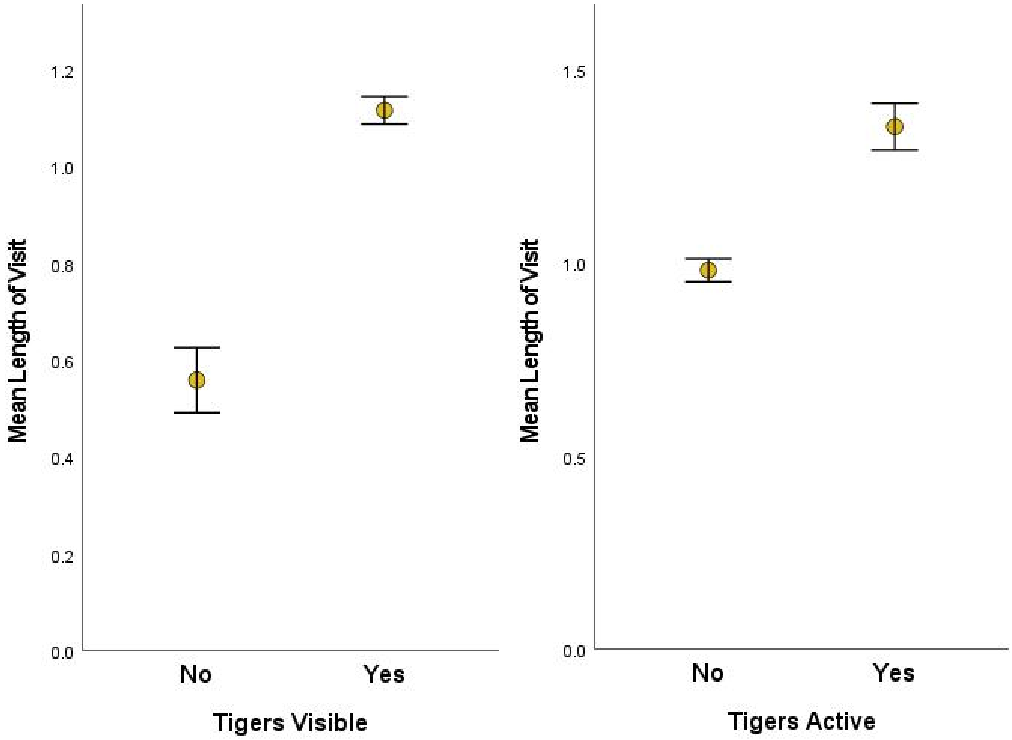

Figure 8: The Effect of Tiger visibility and Tiger Activity on the Mean Length of Visit

As seen in Table 10 the engagement level increased with the number of adults, presence and activity of the tigers, but there was no effect of the weather, number of children nor of the timeframe. Figure 9 shows the significant difference in visitor engagement level when the tigers were active or visible.

Table 10: The Effects of Group Size, Tiger Visibility, Tiger Activity and Timeframe on Visitors' Engagement

	Coefficient	Standard Error	P-value	95% Upper	95% Lower
Number of Adults	0.042	0.017	0.015	0.076	0.008
Tigers Visible	0.490	0.043	<0.001	0.404	0.577
Tigers Active	0.379	0.037	<0.001	0.304	0.453
Timeframe[1]					
Before-During	0.145	0.044	0.001	0.232	0.059
Before-After	0.204	0.047	<0.001	0.295	0.112
During-After	0.058	0.032	0.064	0.120	-0.003

[1] Second one as a reference category

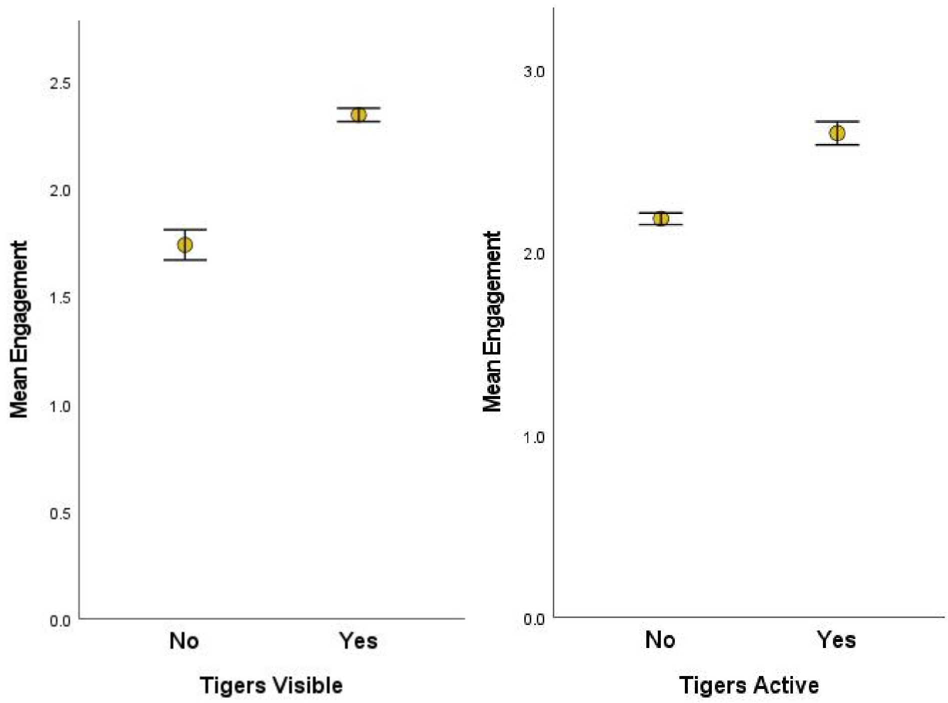

Figure 9: The Effect of Tiger visibility and Tiger Activity on the Mean Level of Visitor Engagement

5. Discussion

5.1. Enrichment Assessment

The findings of this study suggest that olfactory enrichment may not be an effective method of increasing active behaviours. Although, the olfactory enrichment in this study did not have a statistically significant effect on stereotypic and agonistic behaviour, there was an effect on tigers' behaviour. Stereotypic behaviours decreased during the enrichment phase and agonistic behaviour decreased during and after then enrichment phase. It is recommended to further study these scents to determine their effectiveness. There are a couple of factors that may have biased these results. First, during the pre-enrichment data collection of the Sumatran tigers, the female Malayan tiger was in oestrus. Although the two sub-species are not housed in the same enclosure, they are separated by a concrete wall; thus, the Sumatran tigers' behaviour may have been affected. Secondly, even though the time spent recording the tigers' behaviour was random, the enrichment was always placed in the enclosure after feeding around 14.00. Since tigers, like the majority of felids, are primarily nocturnal, 14.00 is not when they are typically their most active. This difference may have influenced how active the tigers were even with the enrichment treatment, and future enrichment studies should take this into account when planning the study. For example, a study by Cederlund (2018) found that tigers tend to have higher interaction with olfactory enrichment in the mornings when compared to other times of the day. Being fed right before the enrichment was offered may have caused more lethargy.

This study also examined the individual tigers' behaviour. During the enrichment assessment, there was not a significant difference in the tigers' behaviour. All individuals had an increase in inactive behaviours and a decrease in active behaviours during the enrichment days. However, there was a significant difference in individual approach time; Cinta approached the enrichment items significantly slower than Falco and Johann. From visual observations, the enrichment items seemed to make Cinta nervous. She would frequently return to the outdoor enclosure after being fed, slinking, or walking quickly with her abdomen close to the ground when novel enrichment items had been added. Although it was not a significant difference, Cinta also had the lowest interaction time with the enrichment objects. These results reflect the ideas presented by Clayton and Shrock (2020) that individual personality and enrichment preference should be taken into account by zookeepers and caretakers when designing enrichment treatments. It is essential to address that these evaluations take the time that a zookeeper or animal caretaker may not have available therefore zoos and other facilities should take enrichment evaluations into account when planning an enrichment regime (Maple & Perdue 2013).

5.2. Odours

The results from the olfactory enrichment showed that overall, there is not a significant difference between animal-based and plant-based olfactory treatments. Although the effects of enrichment type on agonistic, stereotypic, and active behaviour were not statistically significant, stereotypic behaviour was lower during the fish oil and rosewater treatments than before the enrichment. There was a statistically significant decrease inactive behaviour before the enrichment than with the any of the enrichment odours. Interestingly, the conspecific enrichment did not cause an increase in active behaviour. Further study and a larger sample size would be needed to determine if these odours are beneficial to tigers' wellbeing.

Although the results were not significant, the enrichment odour with the fastest average approach time was rosewater, and the slowest was fish oil. Interaction time also was not significantly different between the enrichment types. However, the longest average interaction time was with fish oil, and the lowest was the conspecific odour.

While there were no statistically significant differences in approach time between enrichment types, the enrichment odour with the fastest average approach time was rosewater, and the slowest was fish oil. Fish and conspecific odours may be found within the daily routine of the zoo, and rosewater is not. Therefore, the fast approach time may be due to novelty, as suggested by Veasey (2020). This theory is supported by the interaction time, as rosewater did not induce a long interaction time with the enrichment object. enrichment novelty and avoid habituation (Tarou & Bashaw 2006)

As with approach time, there was not a statistically significant difference in interaction time between the enrichment types. The longest average interaction time was with fish oil enrichment, and the lowest was with conspecific odour. This result may be because the odour was similar to food items.

5.3. Enrichment Presentation

The different enrichment displays lead to a statistically significant decrease in active behaviour with the wicker ball presentation and ground presentation, and an increase in inactive behaviour with enrichment displayed on a box and the ground. Unfortunately, there was not a significant effect on stereotypic and agonistic behaviours.

Although the results are not significant for the enrichment display and the approach time or the enrichment display and the interaction time, the results show slight preferences. For example, the box enrichment display had both the fastest approach time and longest interaction time. While the ground display had both the slowest average approach time and shortest interaction time. There are a couple of reasons that the ground enrichment seemed to be less appealing to the tigers. First, it may have been harder to locate since there was no visible object within the enclosure. Secondly, since there was not a visible object, it might have been less visually interesting.

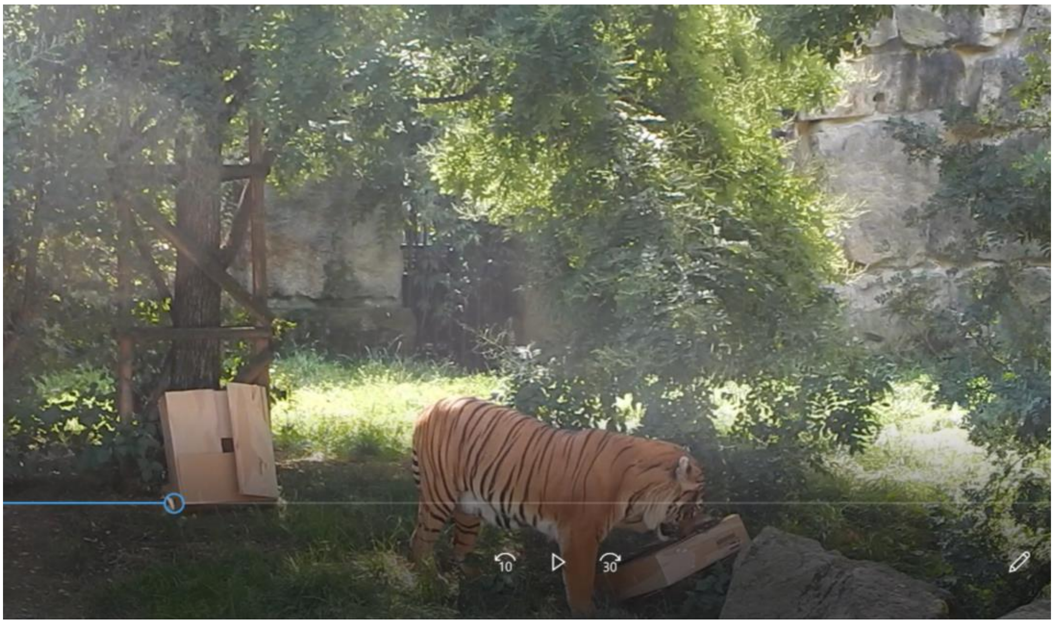

Figure 10: Johann Interacting with the Odorized Enrichment

Salas et al. (2021), states that the enrichment appearance matters less than the behaviour elicited; thus, zookeepers can use various basic enrichment displays as long as they produce the desired behaviours. This study shows that there may be a difference in tigers' behaviour when different display items are used. Albeit many of these results may not be significant, due to the low sample size and technical problems collecting the data, the effects of olfactory enrichment and presentation on tigers' behaviour merits further study.

5.4. Visitor Assessment

The length of time spent at the enclosure and the engagement with the animals increased with the number of adults, presence, and activity of the tigers. The number of children also affected how long the group stayed at the enclosure. The increase in engagement and time spent at the enclosure aligns with results from the previous studies (Davey et al. 2005; Powell & Bullock 2014; Salas et al. 2021); when the tigers are more visible and active, it stimulates a conversation, picture taking, and observation. Whereas when the tigers are inactive or not visible in the enclosure, visitors spend less time and are less engaged. Active behaviours can be elicited through environmental enrichment, as shown by a vast number of studies such as those conducted by Skibiel et al. (2007); Van Metter et al. (2008); Szokalski et al. (2012); Damasceno et al. (2017). Considering that environmental enrichment aims to promote more exploratory and active behaviours, it can be concluded that environmental enrichment will increase both visitor engagement and time spent at the enclosure. However, that was not the case in this study, since the enrichment decreased the time tigers were active, the visitor engagement and length of time observing the tigers decreased as well.

In previous studies, enrichment promoted stronger "encounter" responses in visitors and scored higher in positive attitudes on surveys when the animals exhibited increased species-specific and active behaviours (Powell & Bullock 2014; Salas et al. 2021). The increase in visitor engagement leads to a more positive visitor experience, a better connection with the animals, and a higher opinion of the facility as a whole (Consorte-McCrea 2019). This study showed that the timeframe did not affect visitor engagement nor the length of time spent at the enclosure. Although the timeframe did not affect visitor engagement and the length of visit, it did reflect the tigers' behaviour. When the tigers were more active before the enrichment treatment, it led to higher engagement and time spent observing the tigers. When the tigers were less active during the enrichment, and after the enrichment treatment, the level of engagement and length of stay similarly decreased.

A larger number of children in a group affected the time spent at the enclosure but not the engagement. This result could be due to the enclosure design; in both enclosures, there is a raised platform where the tigers frequently rested, and the best visitor viewpoint is from behind a wooden wall with holes cut into it. These holes are too high for many children to view independently, so the adults in the group needed to lift each child to see the tigers. With many children, the adults needed to lift more children up and thus spent more time at the enclosure. The engagement did not necessarily increase because the children only glanced at the tigers before being set back on the ground. In contrast, a group with a higher number of adults increased both the length of time and the engagement. This difference could be because the adults can see the tigers independently, so when the length of time increased, they were also more engaged.

6. Conclusions

Despite the shortcoming of this study, there are important takeaways for zoos, zookeepers, and animal caretakers, namely that visitor engagement and length of time spent observing the tigers significantly increases when the tigers are active. A couple of suggestions for zoos, zookeepers and animal caretakers are described in the following paragraphs.

The fact that olfactory enrichment did not seem greatly beneficial to the individuals in this study, but has been proven beneficial to other tiger and felid species, shows the importance for zookeepers and animal caretakers to not only evaluate the overall environmental enrichment effectiveness but its effectiveness to the individual level. It is important that zookeepers and animal caretakers should take individual preferences into account when they are designing their enrichment regime. Enrichment evaluations take the time that a zookeeper or animal caretaker may not have available so, it is encouraged that zoos and program directors evaluate their facility's needs and constraints to address this issue.

Secondly, it is recommended that zookeepers and animal caretakers provide a wide selection of scents and presentation options to increase the enrichment novelty and avoid habituation. Since there was not a great difference between the enrichment presentation, the enrichment's appearance matters less than the behaviour elicited. The items in this study were not expensive or difficult to acquire; therefore, they should fit in the budget and time constraints of most enrichment programs.

The third recommendation is to alter the time of day the enrichment is presented. The enrichment items in this study were always offered after the feeding time, and the activity level of the individuals decreased during the enrichment phase. Since tigers are naturally nocturnal midday enrichment directly after eating may have caused more lethargy than in other times of the day.

Zoos play a primary role in establishing a solid connection with nature, reducing fear and human-wildlife conflicts in their communities (Consorte-McCrea 2019). Using environmental enrichment is beneficial to the animals and creates a more engaging and positive experience for the visitors. Therefore, by planning, implementing, and evaluating environmental enrichment programs zoos can, not only create a better environment for the animals in their care, but they start a compelling dialogue with the visitors.

7. References

Boissoneault, L. (2015) *Leopards, Hippos, and Cats, Oh My! The World's First Zoo*. JSTOR Daily. https://daily.jstor.org/leopards-hippos-cats-oh-worlds-first-zoo.

Breton, G., & Barrot, S. (2014) Influence of enclosure size on the distances covered and paced by captive tigers (*Panthera tigris*). *Applied Animal Behaviour Science*, 154, 66–75.

Carlstead, K., & Shepherdson, D.J. (2000) Alleviating stress in zoo animals with environmental enrichment. In: Moberg, G.P., & Mench, J.A., (eds.), *The Biology of Animal Stress: Basic Principles and Implications for Animal Welfare*. New York: CABI Publishing, pp 337-354.

Cederlund, J. (2018) Behavioural responses of Amur tigers (*Panthera tigris altaica*) and African lions (*Panthera leo*) to conspecific urine and to a component of tiger marking fluid [MSc. Thesis]. Linköping University, Linköping.

Clayton, M., & Shrock, T. (2020) Making a Tiger's Day: Free-Operant Assessment and Environmental Enrichment to Improve the Daily Lives of Captive Bengal Tigers (*Panthera tigris tigris*). *Behavior Analysis in Practice*, 13, 883–893.

Clubb, R., & Mason, G. (2003) Captivity Effects on Wide-Ranging Carnivores. *Nature*, 425, 473–474.

Clubb. R., & Mason, G. (2007) Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. *Applied Animal Behaviour Science*, 102, 303–328.

Consorte-McCrea, A., Fernandez, A., Bainbridge, A., Moss, A., Prévot, A., Clayton, S., Glikman, J.A., Johansson, M., López-Bao, J.V., Bath, A., Frank, B. & Marchini, S.

(2019) Large carnivores and zoos as catalysts for engaging the public in the protection of biodiversity. *Nature Conservation*, 37, 133–150.

Dacres, K. (2007). *Panthera tigris*. Animal Diversity Web. University of Michigan. Michigan, USA. https://animaldiversity.org/accounts/Panthera_tigris.

Damasceno, J., Genaro, G., Quirke, T., McCarthy, S., McKeown, S. & O'Riordan, R. (2017) The Effects of Intrinsic Enrichment on Captive Felids. *Zoo Biology*, 36, 186–192.

Davey, G., Henzi, P., & Higgins, L. (2005) The Influence of Environmental Enrichment on Chinese Visitor Behavior. *Journal of Applied Animal Welfare Science*, 8, 131–140.

De Rouck, M., Kitchener, A. & Law, G. (2005) A comparative study of the influence of social housing conditions on the behavior of captive tigers (*Panthera tigris*). *Animal Welfare*, 14, 229-238.

Furlong, E., Gaskill, B., & Erasmus, M. (2021) *Exotic Feline Enrichment*. Purdue Extension. www.extension.purdue.edu/extmedia/AS/AS-675-W.pdf.

Godinez, A., Fernandez, E., & Morrissey, K. (2013) Visitor Behaviors and Perceptions of Jaguar Activities. *Anthrozoös*, 26, 613–619.

Gardiánová, I., & Bolechová, P. (2014) Tigers Stereotypic Pacing and Enrichment. *Annual Research & Review in Biology*, 4, 1544–1550.

Gomes, D., McSweeney, L., & Santos, M. (2019). Effects of Environmental Enrichment Techniques on Stereotypical Behaviours of Captive Sumatran Tigers: A Preliminary Case Study. *Journal of Animal Behaviour and Biometeorology*, 7, 144–148.

Goodrich, J., Lynam, A., Miquelle, D., Wibisono, H., Kawanishi, K., Pattanavibool, A., Htun, S., Tempa, T., Karki, J., Jhala, Y., & Karanth, U. (2015) *Panthera tigris*. The IUCN Red List of Threatened Species 2015: e.T15955A50659951. https://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T15955A50659951.en.

Google Maps. *Google*. maps.google.com.

Gusset, M., & Dick, G. (2011) The global reach of zoos and aquariums in visitor numbers and conservation expenditures. *Zoo Biology*, 30, 566-569.

Hayward, M., Jedrzejewski, W., & Jêdrzejewska, J. (2012) Prey preferences of the tiger Panthera tigris. *Journal of Zoology*, 286, 221–231.

Höttges, N., Hjelm, M., Hård, H., & Laska, M. (2019) How Does Feeding Regime Affect Behaviour and Activity in Captive African Lions (Panthera Leo)? *Journal of Zoo and Aquarium Research*, 7, 117–125.

Kroshko, J., Clubb, R., Harper, L., Mellor, E., Moehrenschlager, A., & Mason, G. (2016) Stereotypic Route Tracing in Captive Carnivora Is Predicted by Species-Typical Home Range Sizes and Hunting Styles. Animal Behaviour, 117, 197–209.

Li-wei, T., Feng, L., & Zhen-sheng, L. (2002). Behavior observation of Amur tiger (*Panthera tigris altaica*) in captivity. *Journal of Forestry Research*, 13, 241-244.

Maple, T., & Perdue, B. (2013) Chapter 6 Environmental Enrichment Zoo Animal Welfare. In: Maple, T., Perdue, B. (Eds.), *Zoo Animal Welfare*. Berlin: Springer Berlin, pp. 95-117.

Mason, G. (2006) Stereotypic Behaviour in Captive Animals: Fundamentals and Implications for Welfare and Beyond. In: Mason, G., & Rushen, J. (Eds.), *Stereotypic* *animal behaviour: fundamentals and applications to welfare*. Wallingford, UK; Cambridge, USA: CABI Publishing, pp 325-356.

Mellen, J., & Shepherdson, D. (1997) Environmental enrichment for felids: an integrated approach. *International Zoo Yearbook*, 35, 191–197.

Miller, L. (2012) Visitor Reaction to Pacing Behavior: Influence on the Perception of Animal Care and Interest in Supporting Zoological Institutions. *Zoo Biology*, 31, 242–248.

World Wildlife Fund. (2014) *More Tigers in American Backyards than in the Wild*. Washington DC, USA: World Wildlife Fund. https://www.worldwildlife.org/stories/more-tigers-in-american-backyards-than-in-the-wild.

Moreira, N., Brown, J., Moraes, W., Swanson, W., & Monteiro-Filho, E. (2007) Effect of housing and environmental enrichment on adreno-cortical activity, behavior and reproductive cyclicity in the female tigrina (*Leopardus tigrinus*) and margay (*Leopardus wiedii*). *Zoo Biology*, 26, 441–460.

Prague Zoo. (2021) *Prague Zoo*. Prague, Czech Republic: Prague Zoo. https://www.zoopraha.cz/en.

Pitsko, L.E. (2003) Wild Tigers in Captivity: A Study of the Effects of the Captive Environment on Tiger Behavior. Virginia Polytechnic Institute and State University of Blacksburg.

Podturkin, A., & Papaeva, N. (2020) Development of an environmental enrichment programme: A case study with a white Bengal tiger (*Panthera tigris bengalensis*) and a jaguar (*Panthera onca*) at Moscow Zoo. *Journal of Zoo and Aquarium Research*, 8, 139-145.

Powell, D., & Bullock, E. (2014) Evaluation of Factors Affecting Emotional Responses in Zoo Visitors and the Impact of Emotion on Conservation Mindedness. *Anthrozoös*, 27, 389-405.

Reiger, I. (1979) Scent Rubbing in Carnivores. *Carnivore*, 2, 17 -25.

Rutledge, K., Ramroop, T., Boudreau, D., McDaniel, M., Teng, S., Sprout, E., Costa, H., Hall, H., & Hunt, J. 2011. *Zoo*. Washington DC, USA: National Geographic. https://www.nationalgeographic.org/encyclopedia/zoo.

Salas, M., Laméris, D., Depoortere, A., Plessers, L., & Verspeek, J. (2021) Zoo Visitor Attitudes Are More Influenced by Animal Behaviour than Environmental Enrichment Appearance. *Animals*, 11, 1971.

Sajjad, S., Farooq, U., Anwar, M., Khurshid, A., & Bukhan, S. (2011) Effect of captive environment on plasma cortisol level and behaviour al pattern of Bengal tigers (*Panthera tigris tigris*). *Pakistan Vet Journal*, 31, 195–198.

Saskia, J., & Schmid, H. (2002) Effect of Feeding Boxes on the Behavior of Stereotyping Amur Tigers (*Panthera Tigris Altaica*) in the Zurich Zoo, Zurich, Switzerland. *Zoo Biology*, 21: 573–584.

Schmidt, T. (2012) Get to know your Animals through Enrichment, an Ocelot Study Case. *The Shape of Enrichment*, 21, 4-5.

SeaWorld Parks. (2021) *Senses. All About Tigers*. Orlando, USA: SeaWorld Parks & amp; Entertainment, Inc. www.seaworld.org/animals/all-about/tiger/senses/

Skibiel, A., Trevino, H., & Naugher, K. (2007) Comparison of Several Types of Enrichment for Captive Felids. *Zoo Biology*, 26, 371–381.

Sommerville, B.A., & Broom, D.M. (1998) Olfactory awareness. *Applied Animal Behaviour Science*, 57, 269–286.

Soso, S., Koziel, J., Johnson, A., Lee, Y., & Fairbanks, W.S. (2014) Analytical Methods for Chemical and Sensory Characterization of Scent-Markings in Large Wild Mammals: A Review. *Sensors*, 14, 4428-4465

Szokalski, M., Litchfielda, C., & Foster, W. (2012) Enrichment for Captive Tigers (Panthera Tigris): Current Knowledge and Future Directions. *Applied Animal Behaviour Science,* 139, 1–9.

Tarou, L., & Bashaw, M. (2006) Maximizing the effectiveness of environmental enrichment: Suggestions from the experimental analysis of behavior. *Applied Animal Behaviour Science*, 102, 189–204.

Tennessen, T. (1989) Coping with confinement – features of the environment that influence animals' ability to adapt. *Applied Animal Behavior Science*, 22, 139–149.

Tripadvisor. 2021. *Prague Zoo - All You Need to Know before You Go (with Photos).* Needham, USA: Tripadvisor. www.tripadvisor.com/Attraction_Review-g274707-d276251-Reviews-Prague_Zoo-Prague_Bohemia.html.

Van Metter, J., Harriger, D., & Bole, R. (2008) Environmental Enrichment Utilizing Stimulus Objects for African Lions (*Panthera Leo Leo*) and Sumatran Tigers (*Panthera Tigris Sumatrae*). *Bios*, 79, 7–16.

Veasey, J. (2020) Can Zoos Ever Be Big Enough for Large Wild Animals? A Review Using an Expert Panel Assessment of the Psychological Priorities of the Amur Tiger (*Panthera tigris altaica*) as a Model Species. *Animals*, 10, 1536.

Veasey, J., Waran, N., & Young, R. (1996) On Comparing the Behaviour of Zoo Housed Animals with Wild Conspecifics as a Welfare Indicator. *Animal Welfare*, 5, 13-24.

Wells, D., & Hepper, P. (2017). The Role of Olfaction in Animal Housing and as Enrichment. In: Nielsen, B (Ed.). *Olfaction in Animal Behaviour and Welfare*. Oxfordshire, UK: CABI Publishing, pp 151–160.

Zug G. *Jacobson's Organ*. Chicago, USA: Encyclopædia Britannica, Inc. www.britannica.com/science/Jacobsons-organ.