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The effect of feeding routines on lions and tigers in a zoo environment

Effekten av fôringsrutiner på løver og tigre i et dyreparkmiljø

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Abstract

This study aimed to investigate the impact of two different feeding routines on the behaviour of lions (*Panthera leo melanochaita*) and tigers (*Panthera tigris tigris*) in a zoo environment. The feeding routines under scrutiny involved a large meal once or twice per week (gorge feeding) compared to smaller daily feedings (control treatment). Observations on a male-female pair of lions and a male-female pair of tigers and their offspring were conducted during a 2-week period with gorge feeding and a 2-week period with daily feeding to evaluate effects of the two feeding regimes on daily activity budgets, stereotyped behaviour and use of enclosure space. The hypothesis was that gorge feeding would reduce stereotyped behaviour and increase natural behaviour compared to daily feeding by reducing the predictability of mealtimes and allowing the animals to feel satiated after eating. Specifically, the predictions were that, when gorge fed, both lions and tigers would exhibit less stereotypic pacing, agonistic behaviour, lying awake with eyes open (versus sleeping), and self-grooming while performing more standing, non-stereotyped locomotion, feeding, and affiliative behaviour compared to when they received daily feeding. It was also expected that their use of enclosure space would vary between the feeding methods, with greater use of the whole enclosure when gorge-fed. Findings revealed significant differences in behaviour and use of space on the two feeding methods. However, the differences varied between the adult lions, the adult tigers, and the young tigers, and also between individuals. Both the tigers, and the lioness, appeared to benefit from gorge feeding. By assessing the relationship between feeding methods and behaviour, this research contributes to discussions on captive big cat welfare and zoo practices. The study highlights the need for further research over extended periods to understand the long-term effects of feeding routines on captive big cat behaviour and welfare. The results emphasize the importance of optimizing feeding practices to enhance animal welfare in zoos.

Sammendrag

Denne studien hadde som mål å undersøke effekten av to ulike fôringsrutiner på adferden til løver (*Panthera leo melanochaita*) og tigre (*Panthera tigris tigris*) i et dyreparkmiljø. Fôringsrutinene som ble vurdert, involverte store periodiske måltider en eller to ganger i uken (gorge feeding) sammenlignet med mindre daglige fôringer (kontrollbehandling). Observasjoner av et hann-hunnpar løver og et hann-hunnpar tigre samt deres avkom, ble gjennomført i løpet av en to-ukers periode med store periodiske måltider og en to-ukers periode med daglig fôring. Dette ble gjort for å evaluere effektene av de to fôringsmetodene på daglige aktivitetsmønstre, stereotyp adferd og bruk av innhegningens plass. Hypotesen var at de store periodiske måltidene ville redusere stereotyp adferd og øke naturlig adferd sammenlignet med daglig fôring ved å redusere forutsigbarheten av måltidstidspunkter og tillate dyrene å føle seg mette etter å ha spist. Spesifikt ble det forventet at både løver og tigre ville vise mindre stereotyp pacing (vandring i mønster), aggressiv adferd, ligging med åpne øyne (i motsetning til søvn), og selvpleie, samtidig som de ville utføre mer stående, ikke-stereotyp bevegelse, fôring og tilknyttende adferd når de ble fôret store periodiske måltider. Det ble også forventet at bruken av innhegningens plass ville variere mellom fôringsmetodene, med mer bruk av hele innhegningen når store periodiske måltider ble praktisert. Resultatene viste signifikante forskjeller i adferd og bruk av plass mellom de to fôringsmetodene, men disse forskjellene varierte mellom voksne løver, voksne tigre og unge tigre, samt mellom individer. Både tigrene og løvinnen, synes å ha hatt fordeler av de store måltidene. Ved å vurdere forholdet mellom fôringsmetoder og adferd, bidrar denne forskningen til diskusjoner om velferden til store kattedyr i fangenskap og praksiser i dyreparker. Studien understreker behovet for videre forskning over lengre perioder for å forstå langsiktige effekter av fôringsrutiner på adferd og velferd hos store kattedyr i fangenskap. Resultatene fremhever viktigheten av å optimalisere fôringspraksis for å forbedre dyrevelferden i dyreparker.

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I finally did it!

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1. Introduction

The welfare of animals in captivity, particularly in zoos, has long been a topic of debate. One of the major concerns is the development of stereotypic behaviour among captive animals, which is often an indicator of poor welfare and stress. Locomotory stereotypic behaviours such as pacing back and forth along a fence line or repeated route-tracing along a defined path are commonly observed in big cats such as lions and tigers in zoos and have raised concerns about the welfare of these animals (Broom, 1991; Mason, 2010). Captive big cats are often subjected to environments that lack the natural resources and stimuli needed to engage in their typical hunting behaviour (Clubb and Mason, 2003; Clubb and Mason, 2007; Kroshko et al., 2016). This can lead to the development of stereotypic behaviours, which are thought to represent a coping mechanism for the stress and boredom associated with captivity (Mellen and Shepherdson, 1997). The presence of stereotypic behaviour in captive animals has been linked to negative impacts on physical and psychological health, including decreased immune function and increased susceptibility to disease (Wielebnowski, 2003).

Lions (*Panthera leo melanochaita*) and tigers (*Panthera tigris tigris*) (Kitchener et al., 2017) are two of the most popular big cats found in zoos worldwide. These animals are carnivores and have unique feeding ecologies, including hunting and scavenging over large areas in the wild. Zoos are unable to provide them with access to such large areas and the limited space in zoos has been associated with the development of locomotor stereotypies in these species in captivity (Clubb and Mason, 2003; 2007). In zoos, their feeding routines are also often far from natural, which may contribute to the development of stereotypic behaviour (Clubb and Mason, 2016). While they would hunt large mammals in nature, it is considered unethical to allow them to hunt and kill live prey in captivity, making it necessary to provide dead prey. Understanding the relationship between zoo feeding routines and stereotypic behaviour is crucial for promoting the welfare of these big cats in captivity.

1.1 Predatory behaviour of big cats in the wild

Lions and tigers in the wild are adapted to preying on large mammals that will sustain them for a relatively long period of time (Seidensticker and McDougal, 1993; Druce et al., 2004).

Because large prey is difficult to catch, they never know when another hunt will be successful. These big cats are opportunistic but also must assess if a potential prey animal is worth spending their energy on trying to catch (Druce et al., 2004; Karanth and Sunquist, 1995).

1.1.1 Natural feeding behaviour of lions

In the wild, lions are known for their strategic hunting tactics, where they work together to bring down large mammalian prey (Schaller, 1972). Lions often live in prides, consisting of several females and a few males, and each pride has a defined territory that they mark with urine, faeces and scratch marks (Funston et al., 2003). While young females usually stay in the pride with their mother, young males leave the pride when they are two to three years old. They then live with their brothers or join other males in a coalition until they are at least 5 years old, when they cooperate to take over a pride. When hunting, lions are selective and, if available, will target prey that are weak, sick, or injured (Smith et al., 2007). Hunting takes a lot of energy, and lions need to ensure that their efforts will result in a successful kill often enough to sustain them and their offspring. Once a kill is made, the social hierarchy of the pride comes into play during feeding (Funston et al., 2003). The male lions are usually the first to feed, followed by the females and cubs (Schaller, 1972). Lions will typically feed several times a day on the same carcass, with each feeding session lasting several hours (Pusey et al., 1997). The amount of time lions spends feeding on a large kill varies depending on the size of the prey (Amorós et al., 2020) and the number of lions present, with some kills being completely consumed within a day, while others can last up to a week (Funston et al., 2003). The species reported to be hunted most frequently by African lions in the wild are wildebeest, zebra, impala, warthog, juvenile giraffes, and buffalo, and it is seen that lions usually go for prey weighing around 100-230 kg or smaller (Funston et al., 2003). Feeding time on a single carcass can also vary depending on external factors such as the presence of scavengers or threats from other predators (Kruuk, 1972). Lions are also known to frequently steal prey killed by hyenas and other species (Watts and Holekamp, 2008).

1.1.2 Natural feeding behaviour of tigers

Tigers are solitary hunters and typically hunt alone to bring down their prey (Goodrich et al., 2010). They are territorial, and like lions, they mark their territory with urine, faeces, and scratch marks. However, they will tolerate the presence of other tigers when they cross paths (Goodrich et al., 2010). The males live alone while offspring are raised by their mother. They

are weaned from milk by around 6 months of age but typically remain with her until they are at least two years of age because they depend on her to bring them prey until they become proficient hunters themselves. Tigers are known to be opportunistic hunters, and their diet includes a variety of prey species such as deer, wild boar, and smaller mammals like hares and rabbits (Sunquist and Sunquist, 2014). Once a tiger has killed its prey, it will feed until it is satisfied, and then it will move away from the kill site to rest and digest its meal (Sunquist and Sunquist, 2014). The amount of time a tiger spends feeding on a large kill can vary depending on the size of the prey and the tiger's hunger level. For example, a study by Goodrich et al. (2010) reported that a male tiger spent 10 hours feeding on a 280 kg adult male wild boar, while a female tiger spent 4 hours feeding on a 27 kg sika deer. In addition, tigers have been observed to revisit a kill over several days, continuing to feed on it until it has been fully consumed (Goodrich et al., 2010). This behaviour conserves energy and reduces the need to hunt frequently (Seidensticker and McDougal, 1993).

1.2 Feeding of big cats in a zoo environment

Feeding routines for big cats in zoos are often designed around providing small meals distributed throughout the day in a controlled environment (Koolhaas et al., 1999). This approach aims to reduce aggression and conflicts between animals, as well as aiming to ensure that each animal receives its required amount of food (Bassett and Buchanan-Smith, 2007). Feeding relatively frequent small meals also allows for close monitoring of the animals' feeding behaviours and can help keepers to detect any changes in appetite, which can be an indicator of underlying health issues (Wielebnowski, 1999). In some cases, zoos acquire food from sources where the meat is not fit for human consumption, such as roadkill, or ethically sourced animals that have died of natural causes (Mellen and MacPhee, 2001). However, the diet and feeding practices in zoos have been a topic of debate among animal welfare advocates. Some argue that the captive environment and frequent small meals is not conducive to the natural feeding behaviours of big cats and may contribute to the development of stereotypic behaviour such as pacing (Carlstead et al., 1993). Others suggest that limited variety in their diet and feeding routine may lead to nutritional deficiencies and result in health problems (Mellen and MacPhee, 2001).

In recent years, there has been a growing interest in incorporating more natural feeding behaviours and enrichment activities into the captive environment of small cats (Shepherdson et al., 1993), as well as big cats such as lions and tigers (Bashaw et al., 2003). This includes

providing a varied diet, feeding whole carcasses, and encouraging natural hunting behaviours, such as hiding food or using puzzle feeders (Mellen and MacPhee, 2001).

1.3 Stress factors for large carnivores in captivity

One of the primary stress factors for large carnivores in captivity is the size of the enclosure relative to their home range size in the wild. Studies have found that animals housed in enclosures that are smaller than their natural home range size are more likely to display stereotypic behaviours such as pacing, circling, and other repetitive movements (Clubb and Mason, 2003; Clubb and Mason, 2007; Harper et al., 2016). This can indicate that the animals experienced boredom and frustration related to lack of engagement in hunting for prey for a large proportion of their active day. Another stress factor for large carnivores in captivity is social interaction with conspecifics in the same enclosure. For species that would typically be solitary in the wild, such as adult tigers without offspring, housing them together can promote aggression and conflict, which is associated with stress and even physical harm (Wielebnowski, 2003). The smell of prey in neighbouring zoo enclosures may also be a stress factor for large carnivores in captivity. The scent of live prey can be enticing to predators and can cause them to become agitated and frustrated if they are unable to access it (Wielebnowski, 2003). Another cause for stress can be noise from people and entertainment in the zoo. Loud noises and crowds may be overwhelming for animals adapted to quiet and solitude in the wild (Wielebnowski, 2003).

1.4 Stereotypic and other behaviours of captive felids

In captive environments, felids are prone to developing stereotypic behaviours which have been associated with negative impacts on their welfare (Clubb and Mason, 2003). Stereotypic behaviours can manifest in different ways, including route tracing (e.g. circling, linear pacing or the following of any fixed, repeated path), stationary (i.e. performed in one spot, for example digging, rocking, head rolling) or oral (i.e. involving jaws, tongue and/or lips, e.g. sucking, fur chewing, regurgitation) (Kroshko et al., 2016). These behaviours can be observed before, during, and after feeding sessions to evaluate the effects of different feeding routines on the animals' welfare. A study by Lyons et al. (1998) on nine felid species showed that feeding regime affected stereotypic pacing. Pacing tended to be more apparent on fasting days, and before feeding on daily feeding days. Shepherdson et al. (1993) found that captive Mainland leopard cats (*Prionailurus bengalensis*) showed less stereotypic pacing when predictability of

food was decreased. Another study looked at big cats' activity budgets before, during, and after providing food enrichment, with a focus on activity levels, frequency and variety of feeding behaviours, and occurrence of stereotypic behaviours (pacing) (Bashaw et al., 2003). There was a slight decrease in stereotypic pacing by lions and Sumatran tigers (*P. tigris sumatrae*) when being fed fresh fish, and a big decrease when being fed a horse leg which lasted several days (Bashaw et al., 2003). Pitsko (2003) reported that captive tigers showed less stereotypic pacing when placed in a more naturalistic enclosure compared to a less naturalistic enclosure and suggested that tigers be housed in large enclosures with a variety of enrichments, vegetation, and other accommodations to reduce stress. Rouck et al. (2005) found that when a female tiger was housed in an enclosure with another female tiger and with no other tigers in neighbouring enclosures, less pacing was observed. They saw that when the tigers were housed with more than two tigers in one enclosure, and with neighbouring enclosures housing tigers, they showed more pacing. Having tigers in neighbouring enclosures with the animals able to see each other appeared to cause frustration and more stereotypical pacing. Mallapur and Chellam (2002) also showed that stereotypic pacing was affected by enclosure type in captive leopards (*Panthera pardus*), being higher in an off-exhibit (indoor) enclosure than an on-exhibit (outdoor) enclosure.

It is important to measure a range of behaviours to obtain a complete picture of the animals' welfare status. For each behavioural trait, it needs to be clear why it is being measured, what is being predicted, and why (Kroshko et al., 2016). The levels of exploring different areas of an enclosure, aggression, and time spent resting have been investigated in captive lions, tigers, and other big cats. In captive leopards (which are solitary cats like the tiger) held in groups of two or three, the paired animals usually avoided each other whereas the trio showed more interaction and preferred to use the same locations of the enclosure at the same time (Quintavalle et al., 2021). The male of the trio showed aggressive and affiliative behaviour towards the others suggesting a sex combability effect (Quintavalle et al., 2021). Miller and Kuhar (2007) saw signs that housing a relatively large group of tigers (6 female tigers housed together) may lead to more non-contact aggression, which could lead to more serious forms of contact aggression. This could result in serious wounding, causing them to conclude that tigers should be housed in smaller groups of 3-2 tigers to minimise aggression. This was because tigers are solitary animals in the wild and not adapted to socializing with many tigers at once, but housing tigers alone in captivity can be challenging because of the limited space and lack of possibilities to keep all the animals separated. In their study on lions and tigers,

Bashaw et al. (2003) found that both species spent the same amount of time resting, and that time of day had a big impact on resting behaviour. Across three observation periods per day, the animals spent more time resting during the midday (12:00-14:00) and afternoon (14:00-16:00) periods compared to the morning period (10:00-12:00). They also saw that the lions preferred to rest off-exhibit (indoors) than on-exhibit (outdoors), and that the tigers showed less pacing in a bigger exhibit compared to a smaller exhibit.

1.5 Gorge feeding of captive felids

A gorge feeding schedule is a feeding method that simulates natural feeding and has been referred to as a form of enrichment for captive lions and tigers compared to daily feeding of a smaller meal (Altman et al., 2005). Gorge feeding means providing a large carcass to the animals on a random feeding day to give them a big meal and reduce the expectation of feeding (Bond and Linburg, 1990). Lions in the wild do not eat every day or on a fixed interval, but rather eat every 2.5-3.5 days depending on their habitat and hunting success rate (Schaller, 1972). Wild tigers will also not eat every day in the wild, and they will typically eat one large prey once a week, also depending on success rate of the hunt (Sunquist, 2010). According to Altman et al. (2005), a gorge feeding schedule led a lion to show improved nutritional status and increased activity, with a decrease in behaviours such as agonistic behaviour and pacing, but an increase in active appetitive behaviours. Bond and Lindburg (1990) found that cheetahs (*Acinonyx jubatus*) fed carcasses instead of small meals showed improved appetite, longer feeding bouts and greater possessiveness of food, as well as improved dental health. They also mentioned the amount of effort involved in obtaining food and pleasure associated with feeding on carcasses. Stark (2005) also found that the presence of carcasses led to an increase in species-appropriate behaviour in tigers in a zoo environment.

1.6 Goal

The goal of this study was to compare the effects of two different feeding routines on the behaviour of captive lions and tigers over time. The impact on their behaviour of being fed a large meal once or twice per week on an unpredictable day (gorge feeding), which is more typical of their feeding pattern in the wild, was compared to feeding a smaller daily meal, which is currently more typical in zoos. Stereotyped pacing, non-pacing locomotion, lying with eyes open (vs sleeping), standing, agonistic behaviour, affiliative behaviour, self-grooming and feeding behaviour were observed and compared during a 2-week period of gorge

feeding and a 2-week period of daily feeding. This allowed for comparison of the effect of the different feeding methods on the daily activity budget. Observations spanned the times before and after feeding. The pre-feeding observations captured anticipation of the animals for food while behaviour after feeding could vary depending on differences in satiety from the feeding methods. By exploring the relationship between feeding routines and behaviour, the overall aim was to gain new knowledge that would contribute to the promotion of the physical and psychological well-being of captive lions and tigers.

1.7 Hypothesis

It was hypothesised that the welfare of captive lions and tigers would be improved by giving a large meal once or twice per week on unpredictable days (gorge feeding) rather than small daily meals (control) by reducing the predictability of mealtimes and allowing the animals to feel satiated after eating.

1.8 Predictions

It was predicted that, when gorge fed, both lions and tigers would exhibit less stereotypic pacing, agonistic behaviour, lying awake with eyes open (vs sleeping), and self-grooming while performing more standing, non-stereotyped locomotion, feeding, and affiliative behaviour compared to when they received daily feeding. It was also expected that their use of enclosure space would vary between the feeding methods, with gorge feeding leading to more roaming over the whole enclosure instead of staying near the feeding area.

2. Methods

2.1 Animals, housing, and management

The study was conducted on the behaviour of one group of lions of the subspecies found in southern and eastern Africa (*P. leo melanochaita*) and one group of tigers of the mainland Asia subspecies (*P. tigris tigris*) at Dyreparken, a zoo in Kristiansand, Norway, during February of 2023.

The lion group consisted of one adult male and one adult female who were approximately 3 years old, along with their four 4-5-month-old cubs (one female and 3 males), that were occasionally still getting milk from the lioness. Observations were focussed on the two adult lions.

The lion enclosure consisted of an outdoor area, an indoor area with public viewing windows, and a backstage area where they were fed, given snacks, and given any needed medical care. They had access to water in all areas. Outdoors they had a water feature they could drink from, while inside they had an automatic water bowl that would refill as the animals drank from it. For at least the last 6 months before the study, the lions were accustomed to a regular daily schedule of feeding on 5 days per week as well as receiving a few pieces of meat as a snack given in the backstage area. They were also used to being given chickens, chunks of meat, bones or skin for presentations and were used as a form of enrichment. The main meals and snacks (besides chickens) mostly comprised horse meat. The lioness and cubs were separated from the male during meal feeding throughout the entire study period to ensure adequate food intake by each individual. The separation happened after the meal was placed into two separate backstage cages. The male lion was let into one cage a few seconds before the lioness and the cubs were let into the other cage. The time schedule of the daily feeding varied somewhat depending on the zookeeper's daily work schedule and which zookeeper was at work. After feeding, the lions were let back out into the indoor area and could walk back and forth from the backstage area and indoor area as they pleased. There were only a few exceptions to this when the zookeepers did maintenance or cleaning of the backstage cages. At night, the lions stayed inside in the indoor area with access to the backstage area, and in the mornings the adult lions had the option of going outside, usually around 09:00 am.

The tiger group consisted of a 13-year-old adult male and a 13-year-old adult female who had three 18-month-old cubs (two males and one female). The tigers had an outdoor area, indoor area with public viewing windows, a small outdoor enclosure, and backstage area for feeding and medical care. If the tigers were in the indoor area, they could also have access to the backstage area and the small outdoor enclosure. The tigers had access to water in all areas. The outdoor area had a water feature, and the indoor and backstage areas had automatic water bowls that would refill when the animals drank from them, like the lion water bowls. The tigers had already been started on a gorge feeding schedule before the observations began. On the days with no feeding, the tigers would often get one snack per day outdoors consisting of a chicken, horse bone or horse skin, especially during presentations to the public. The adult female was in heat during the study period and had to be separated from the males as breeding approval from the breeding management team was not immediately obtained. During the daytime, she spent about half the days in the indoor area with access to the backstage and small outdoor area, sometimes together with the female cub while the males were outdoors,

and sometimes by herself in this area while the female cub was together with the males in the main outdoor area. She was switched every other day with the males, so she was in the big outdoor enclosure, often with the female cub, while the males were in the indoor area with access to the backstage area and small outdoor enclosure. During nighttime, all tigers were excluded from the big outdoor area, but the female tiger remained separate from the males, with access to either part of the backstage area and the small outdoor enclosure, or the indoor area and part of the backstage area. This was depending on where the male tigers were placed during nighttime, and it shifted approximately every other night. Because the adult female was not always visible, more observations were made on the adult male and the three cubs than on the adult female.

2.2 Experimental design

Permission was obtained from the zoo to make behavioural observations on the lions and tigers during the month of February 2023. Because all observations were made on existing procedures at the zoo and no invasive procedures were performed to collect the data, it was not required to obtain ethical approval for this behavioural study specifically. For the first half of the study (31st January – 12th February), the lions and tigers were fed on a gorge feeding routine and in the second half (13th – 29th of February), they were given smaller daily meals.

The lions were fed a big meal of horse meat with skin and bones on the 31st of January, 3rd of February, 7th of February and 10th of February at approximately 13:30, with a snack outdoors at 08:30 only on the first day. The meals were fed with the male lion feeding alone, and the lioness and cubs feeding together, in the backstage area. In the second half of February, starting on the 13th of February, they were fed on a daily feeding routine in the backstage area, with separation of the male from the female and cubs. The daily meals were served at 14:00, with a snack outdoors at 08:30 each day, for 6 days. On the 19th of February, they were fed at 15:00 due to a public presentation at 13:00 when they were served a bone (in addition to their morning snack). After this, the daily feeding schedule remained consistent with a snack at 08:30 and the daily meal at 16:00.

The tigers were gorge fed a meal of horse meat and bones on the 31st of January and 7th of February. The adult male and three cubs were fed in the outdoor area at 13:00 on the 31st of January and 16:00 on the 7th of February whereas the adult female was fed in the indoor area a bit later, at 14:00 and a little after 16:00 on these days, respectively. During presentations of

the adult female and female cub at 13:00 on the 4th and 11th of February, and presentations of the adult male and male cubs at 13:00 on the 5th and 12th of February, each tiger was given a chicken (though the adult male did not eat his chicken). Daily feeding for the tigers from the 13th – 29th of February consisted of horse meat, often with a snack as well during the day. The daily meals were given in different backstage cages, one for the adult male, one for the adult female and one or more cages for the offspring, to ensure that all animals got the right amount of food each day. The daily feeding schedule varied greatly depending on the zookeeper's work schedule, with the animals getting fed at 07:50, 08:30, between 13:00 and 15:30, 17:00 and 19:45 on different days.

2.3 Data collection

2.3.1 Observation periods

The lions and tigers were observed on 8 (tigers) or 9 (lions) consecutive days during the gorge feeding period starting on 04.02.23 and on 14 days (both species) during the daily feeding period starting on 14.02.23 and ending on 28.02.23. During the daytime, observations were made during approximately 30-minute sessions at each enclosure during which each animal in the enclosure was located and scanned for behaviour about once every 3 to 5 minutes, before moving to the other enclosure to make scans there. The first observation session in the morning was at the lion enclosure, with subsequent observation sessions alternating between each enclosure. Usually, daytime observations ended at the lion enclosure. There was some variation in the schedule if the zoo scheduled a lion presentation to visitors from 13:00 – 13:30. If so, the tiger observation was skipped at this time and, instead, an extra scan was made of the lions. Because of the size of each enclosure and the possibility that the animals could be located anywhere in the enclosure, sometimes the animals were located and observed directly and at other times they were located and observed remotely via surveillance cameras providing views of the indoor housing area and the backstage area that could not be seen directly. The observer had permission from the zoo to access these cameras via the internet from a mobile phone or laptop. In addition to the daytime observations, two rounds of indirect observations per night were made remotely via the cameras while the animals were shut inside for the night (Table 1).

Table 1. Timetable for observations on lions and tigers. An observation session at each enclosure lasted 30 minutes, when an instantaneous scan sample of each animal was recorded every 3-5 minutes. The green colour background indicates times when scans were usually made. However, during weekends when lion presentations were sometimes made for visitors at 13.00-13.30, the tiger observation at 13.00-13.30 was omitted and an extra observation was made of lions at this time. The orange colour indicates varying times for observations because of presentations or in-person observations ending earlier on some days. The red indicates times with no observations.

Lions	**Tiger**	**Observation method**
08:30 - 09:00	09:30 - 10:00	In person
10:30 - 11:00	11:30 - 12:00	In person
12:15 - 12:45	13:00 - 13:30	In person
13:00 - 13:30 Presentation		In person
14:00 - 14:30		In person
18:30 - 19:00	19:30 - 20:00	Surveillance camera
21:30 - 22:00	22:00 - 22:30	Surveillance camera

The animals were often at different locations and sometimes they were hard to spot if they were moving around a lot, especially when in the big outdoor enclosure. Spots had to be found around the enclosures where the overview of the animals was good. Sometimes it was necessary to move frequently between these spots because of high activity of all or some of the animals. However, each animal had an area that was favoured, making them often easy to find.

Although the zoo staff set up the cameras to give the best view possible, it was not always possible to see all animals when they were indoors, especially in the tiger housing. Three cameras were located inside the lions' indoor area, and one camera in the backstage area. The cameras were controllable, enabling the researcher to follow the animals' movements around the rooms. In the tigers' indoor area, there were two cameras, but one camera showing the indoor area was not operational. Two cameras were also positioned in the backstage area, providing a view of most backstage cages, except for two blind spots. Although a wilderness camera was available for use in the small outdoor enclosure of the tiger area, it was not utilized due to difficulty in finding an optimal spot to capture activity. Therefore, there were some occasions when certain individuals could not be located. The camera set-up allowed for more scans of the lions than the tigers in the backstage area where they were fed and where they could stay during the night.

2.3.2 Instantaneous scan sampling

Instantaneous scan sampling was used to register the animals' behaviour in a quick manner and determine their daily activity budget. During each scan of each animal, its behaviour was categorised according to an ethogram developed based on behaviour typical of lions and tigers in captivity (Stanton et al., 2015) and designed to capture a wide range of behaviours. The ethogram consisted of 9 behaviour categories recorded as occurring (1) or not occurring (0) at the time of observation, plus a miscellaneous Other category that contained relatively infrequent behaviours (Table 2). When a behaviour in the Other category occurred, a letter code was used to record which of the behaviours was being performed. The behaviours were not mutually exclusive. All behavioural data were collected by a single observer using the precise definition of each behaviour to ensure reliability if additional observers would use the same ethogram.

Table 2. Ethogram describing the behaviour categories recorded during instantaneous scan sampling.

Behaviour	**Description**
Lying	Lying on stomach, side or back, sitting or kneeling.
Standing	Standing upright on all four legs, staying in one place. The paw pads are touching the ground holding the body upright.
Locomotion	Moving the legs to go to a new location, alternately lifting and placing each foot on the ground, usually with the body weight on two or more feet at a time when walking. The animal can also perform pacing, run, or jump with a rapid, bounding gait, usually with all four feet off the ground at once.
Pacing	A form of locomotion in which the animal is walking back and forth repeatedly within a confined space. The movement can be along a fence or wall in a linear pattern or follow a more circular or irregular but repeated path. The head may be held high or low. When turning, a head movement like a sway or a jerk may be included in the repetitive pattern of movement.
Agonistic behaviour	Behaviours related to aggression, dominance, or submission. Threat display: animal is showing aggressive postures, such as arching the back, growling, or baring teeth. Aggression: animal is attacking or attempting to attack another animal. Submission: animal is showing deference to a dominant animal, such as crouching or rolling onto its back.
Affiliative behaviour	Behaviours related to social bonding, grooming, or play. Social grooming: an animal is grooming another animal, often using the mouth or tongue to remove dirt and debris from the fur. Play: animal is engaging in playful social behaviours, such as chasing, wrestling, or pouncing on other animals. Affectionate behaviour: animal is showing signs of affection towards another animal, such as nuzzling, licking, or rubbing against the other animal.
Self-grooming	Animal is grooming itself, often using the mouth or paws to clean and groom its fur. Licking: animal is using its tongue to clean and groom its fur. Scratching: animal is using its paws or claws to scratch and groom areas of its body. Rolling: animal is rolling on the ground or rubbing against objects to clean and groom its fur.
Feeding	Includes consuming food, having food in the mouth, or drinking. Chewing food into smaller pieces using teeth and jaws. Swallowing food, using the tongue to push food to the back of the mouth and the muscles of the throat to move the food down the oesophagus. Drinking water or other liquids using the mouth.
Eyes open	This behaviour was evaluated in every scan. Animal's eyes are open and tracking movement or watching the surroundings. Animal may be awake but drowsy. Includes blinking or squinting in bright light.
Other	Comfort: stretching a body part. Explore: directed towards non-food objects, structures, fences, scented spots, enrichment materials, substrate, including sniff, dig, manipulate, lick or chew non-food items. Locomotory play: zoomies, sliding, dangling, bouncy running, jumping up or down playfully, twisting, rolling over playfully (excluding social interaction). Mark: spray, rub head on object, scratch paws on ground or object. Urinate, Defecate, Sexual behaviour, Vigilant: head up alert, listening, watching.

2.3.3 Mapped locations in the enclosures

Maps of each enclosure were made, divided into different zones given different codes (Fig. 1-3). During each instantaneous scan, the code corresponding to the observed animal's location in the enclosure was recorded to document how each animal used the space in the enclosure. There were also areas in both the lion and tiger enclosures where visitors (and the observer) could not see the animals, designed to give the animals the option of privacy from the human audience. The codes Soko, PR, Plains, Top, Hatch and Pres were used for zones in the lions' outdoor enclosure, and the codes Top, Bamboo, WB, DR, Water, Rock, Pres, Hatch and were used for the tiger's outdoor enclosure along with SOE for the small outdoor enclosure that they could use day and night (Fig. 1). The codes UPLOG, Trees, UVW, UVA, Logvw, Dva, Stairs and BR depicted zones in the lions' indoor enclosure (Fig. 2), and the codes for the tigers' indoor area were DVA, UVA, UVW and BR (Fig. 3).

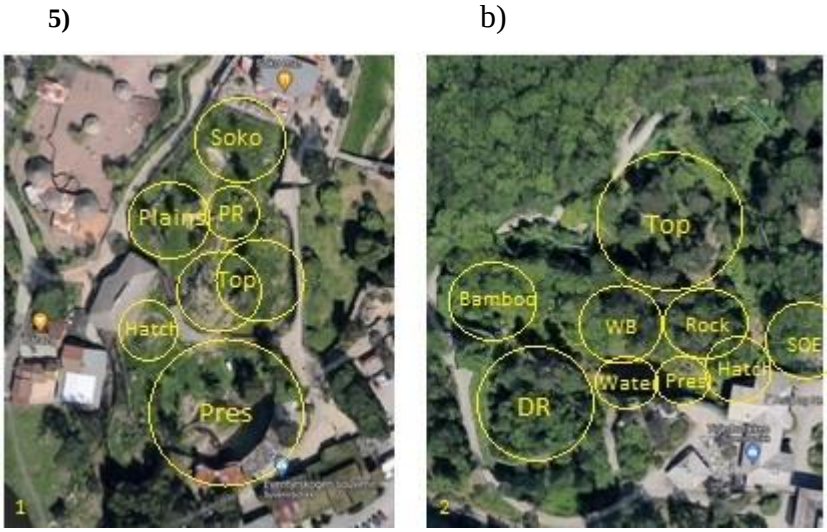

Fig. 1. Map showing (a) the lion enclosure and (b) the tiger enclosure. The images were captured from https://goo.gl/maps/CepwgJyp1ykT4nHa7 and https://goo.gl/maps/CepwgJyp1ykT4nHa7, respectively, on 20.01.2023. The codes denoting different zones within each enclosure are shown in yellow. A) Soko (Area close to soko burger, a restaurant), PR (Pride rock), Top (Highest point in the outdoor enclosure), Pres (Presentation area), Hatch (Close to the hatch leading to the back room), Plains (Bigger area behind pride rock). B) Top (Highest resting point in the outdoor enclosure), WB (Water bank), Rock (a high rock formation behind the presentation area), Pres (Presentation area), Water (the water feature in the enclosure), Dr (Down rock, a rock formation, Bamboo (A cluster of bamboo at one end at the enclosure), Hatch (the hatch leading to the indoor back room area and SOE (Small outdoor enclosure which the animals could also access during nighttime).

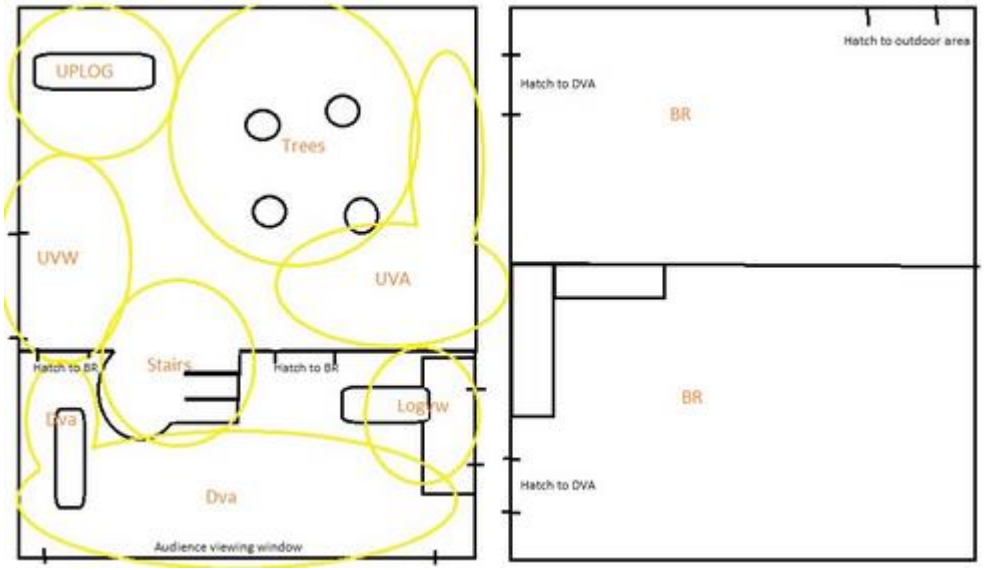

Fig. 2. Indoor area and backstage area for the lions. The codes for each registered location are marked in orange text. UPLOG (a log in the back of the upstairs indoor area), Trees (a formation of upright logs looking like trees), UVW (upstairs viewing window), UVA (upstairs viewing area), Stairs (stairs leading to the upstairs area including a viewing rock), Dva (downstairs viewing area containing a window where the audience could watch the lions), Logvw (log viewing window with a shelf with a log leading up to it), BR (back rooms in the back-stage area viewable via surveillance cameras).

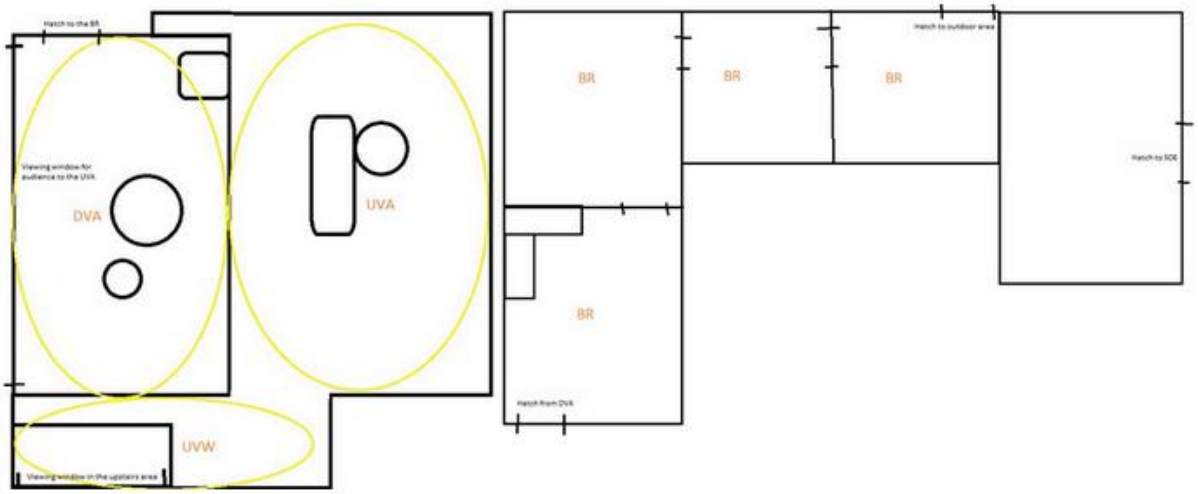

Fig. 3. Indoor area and backstage area for the tigers, with codes assigned to each area marked in orange text. DVA (downstair viewing area), UVA (upstairs viewing area), UVW (upstairs viewing window), BR (back room). Underneath the UVW platform there was a second viewing window for the audience to see the down-stairs viewing area. The sketch of the back rooms forming the backstage area are estimated from the shape of the building and from what could be viewed via surveillance cameras.

2.3.4 Data spreadsheet

To collect the data during the daytime observation sessions at each enclosure, the observed behaviours during scans were recorded on a printed data sheet and the data were later transferred to an Excel spreadsheet. Data collected remotely at night were entered directly into the Excel spreadsheet. Tables 3-5 show examples of data collected in different columns of the spreadsheet. Table 6 shows the number of scans collected on each observed lion and tiger. There were more observations during daily feeding days than gorge feeding days (9 observation days on gorge feeding and 14 observation days on daily feeding with the lions, 8 observation days on gorge feeding and 14 observation days on daily feeding with the tigers) because the gorge feeding started before the observer arrived at the zoo to begin the study.

Table 3. Example of data collected on the adult male tiger, showing the first nine columns of the data spreadsheet. Date represented the date of observation, Time was the time when the tiger's behaviour was scanned, Start time was the start of the observation window from 13.00 to 13.30, Animal was the family member, in this case M for male adult, Species was tiger, Days since eaten was the number of days elapsing since the animals received their last main meal, Feeding time was the most recent date when the animal last ate a main meal, Days since any meal included any extra snacks they received such as a bone during a presentation to visitors, and Feeding method was the method being used on the date of the observation (gorge or daily), which was daily during this example.

Date	Time	Start time	Animal	Species	Days since eaten	Feeding date	Days since any meal	Feeding method
18.02.2023	13:00	13:00	M	TIGER	1	17.02.2023	1	DAILY
18.02.2023	13:03	13:00	M	TIGER	1	17.02.2023	1	DAILY
18.02.2023	13:05	13:00	M	TIGER	1	17.02.2023	1	DAILY
18.02.2023	13:10	13:00	M	TIGER	1	17.02.2023	1	DAILY
18.02.2023	13:13	13:00	M	TIGER	1	17.02.2023	1	DAILY

Table 4. Example of data collected on the adult male tiger, showing columns 10 to 17 of the spreadsheet. Area and Location documented where the animal was located during the scan, based on defined locations on a map of the enclosure, Temperature was the temperature in degrees Centigrade at the start of the 30-minute observation period (from Yr.no), Camera was N for no or Y for yes, depending whether the scan was direct or done using a surveillance camera, and the Rain Snow column indicated if it was raining or snowing during that observation period. N visitors is the estimated number of visitors watching the animals, the Other column contained the letter code for any behaviours in the Other category of the ethogram, and the Comments column was used to add different additional information that could affect interpretation of the recorded behaviour, for example a presentation to visitors or disturbance from a moving vehicle.

Area	Location	Temperature	Camera	Rain Snow(y/n)	N visitors	Other	Comments
Out_in	PRES	4	N	N	50	0	0
Out_in	PRES	4	N	N	50	0	0
Out_in	PRES	4	N	N	50	0	0
Out_in	WATER	4	N	N	50	v	0
Out_in	WATER	4	N	N	50	v	0

Table 5. Example of data collected on the adult male tiger, showing columns 18 to 26 of the spreadsheet. These columns were used to record the behaviour of the animal during each instantaneous scan, based on a binary response of 1 if the animal was performing the behaviour and 0 if not performing the behaviour.

Lie	Stand	Locomote	Pace	Agonistic	Affiliative	Self-groom	Feed	Eyes open
0	1	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	1
1	0	0	0	0	0	0	0	1
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0

Table 6. Distribution of behavioural scans made on each observed animal during the gorge feeding and daily feeding periods. There were some missing data when an animal could not be located, especially during nighttime in the tiger exhibit.

Animal	Gorge	Daily	Total
Lion – Adult male	263	469	732
Lion – Adult female	263	465	728
Tiger – Adult male	286	327	613
Tiger – Adult female	286	327	613
Tiger – Young female	286	327	613
Tiger – Young male 1	286	327	613
Tiger -Young male 2	286	327	613
Total:	1430	1635	3065

2.4 Statistical analysis

The statistical analysis was done using Excel, which was also used to make graphs. Chi-squared tests were used to compare the feeding methods. The chi-squared test is based on the comparison of observed and expected frequencies within a contingency table. The formula used to calculate the chi-squared statistic for the analysis is as follows:

$$\chi 2 = \sum = \frac{(O - E)^2}{E}$$

Where:

- $\chi 2$ represents the chi-squared statistic.
- O is the observed frequency in a particular cell.
- E is the expected frequency in the same cell, calculated based on the null hypothesis of no association between feeding method and behaviour.

The observed frequencies were recorded instances of different behaviours exhibited by lions and tigers under each feeding method during the instantaneous scan samples. The expected frequencies were determined based on the assumption that the behaviours would be observed in a similar proportion of scans regardless of the feeding method. A difference in behaviour between the feeding methods was considered statistically significant if the p-value was less

than 0.05. If expected values were less than 5, Yates' correction was used to calculate the chi-squared statistic and p-value.

3. Results

3.1 Effect of feeding method on behaviour of the adult lions

The two adult lions showed some differences in their behaviour during gorge versus daily feeding as illustrated in Fig 4 (for summary statistics, see Appendix Table 1). Chi-squared tests (Table 7) showed that the differences were significant for the behaviours: lying ($p < 0.001$), total locomotion ($p=0.016$), pacing locomotion as a proportion of total locomotion ($p=0.004$), total eyes open ($p < 0.001$), and lying with eyes open as a proportion of total scans with eyes open ($p=0.002$). The lions showed an increase in overall lying, lying with eyes open, and overall locomotion during daily feeding. On day 6 and day 7 of gorge feeding, there was quite a bit of pacing while during daily feeding days, there was generally a lot of lying without pacing. The difference in scans with eyes open was due to the lioness, who went from 26 % eyes open during gorge feeding to 41 % eyes open during daily feeding, with the difference mainly occurring when lying down (see Appendix Tables 2 and 3 for behaviour results by individual adult lion). The Appendix Table 2 for the male lion shows that the significance in locomotion is due to non-pacing locomotion, and pacing was at similar levels during daily feeding and in gorge feeding. The Appendix Table 3 for the lioness shows no difference in overall locomotion but more pacing during daily ($p<0.001$) than gorge feeding. The proportion of scans spent standing tended to be higher during daily feeding ($p=0.069$) while feeding tended to be higher during gorge feeding (0.093), when the animals had access to bones and scraps during the periods between provision of a new carcass during the gorge feeding. Agonistic, affiliative, and self-grooming behaviour were recorded relatively rarely, and did not differ significantly between feeding methods.

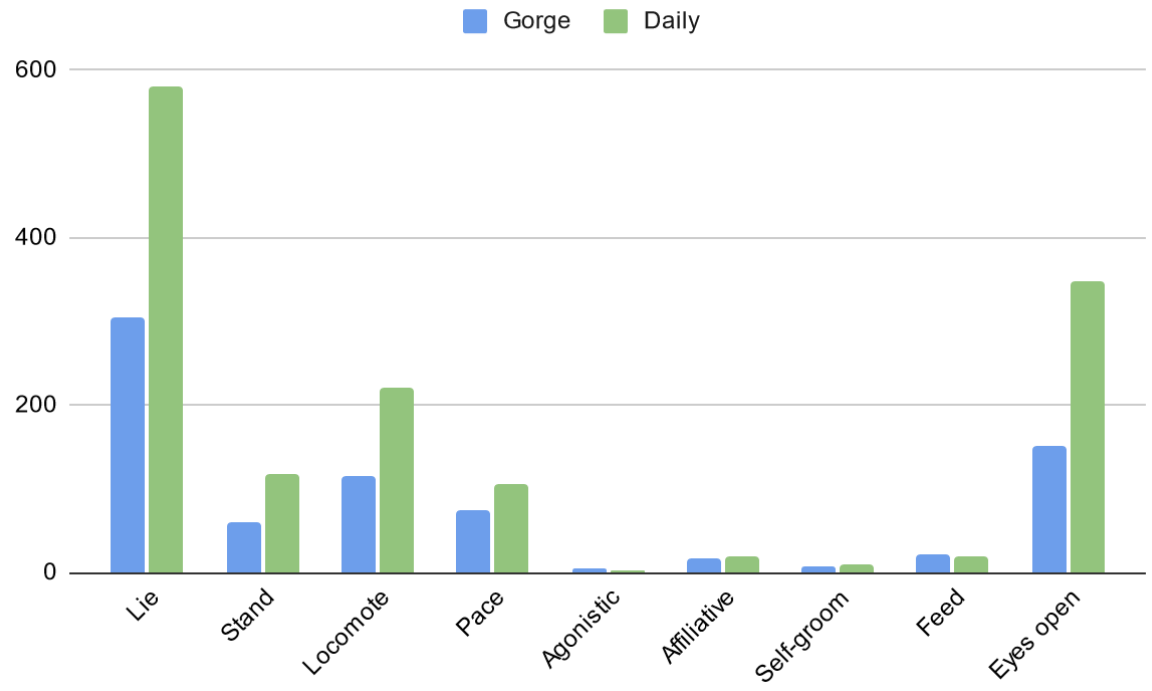

Fig. 4. Average proportion of scans in which each behaviour was performed by the male and female adult lion during gorge feeding versus daily feeding.

Table 7. Chi-squared test results on number of scans in which the adult male and female lion engaged in each behaviour during gorge feeding and daily feeding.

Behaviour	**Gorge feeding (Yes)**	**Gorge feeding (No)**	**Daily feeding (Yes)**	**Daily feeding (No)**	**Total (n scans)**	**Chi-squared**	**P-value**
Lie	305	221	581	466	1318	33.91	**<0.001**
Stand	60	466	118	674	1318	3.30	0.069
Locomote	115	411	220	572	1318	5.83	**0.016**
Pace	74	41	105	115	335	8.39	**0.004**
Agonistic behaviour	4	522	3	789	1318	0.30	0.585
Affiliative behaviour	17	509	20	772	1318	0.58	0.447
Self-groom	8	518	10	782	1318	0.16	0.692
Feed	22	504	20	772	1318	2.81	0.093
Eyes open	151	375	348	444	1318	31.17	**<0.001**
Lie with eyes open	144	161	337	244	886	9.38	**0.002**

3.2 Differences in behaviour of the tigers

3.2.1 Effect of feeding method on behaviour of the adult tigers

A graph comparing the behaviour of the adult male and female tiger on the two feeding methods can be seen in Fig. 5, with chi-squared results in Table 8 and summary statistics in Appendix Table 4. Overall locomotion (p=0.010), pacing locomotion (p=0.026), and feeding (p=0.007) differed between feeding methods. There was less overall locomotion, less pacing, and more feeding during gorge feeding compared to daily feeding, and a tendency for more standing (p=0.076).

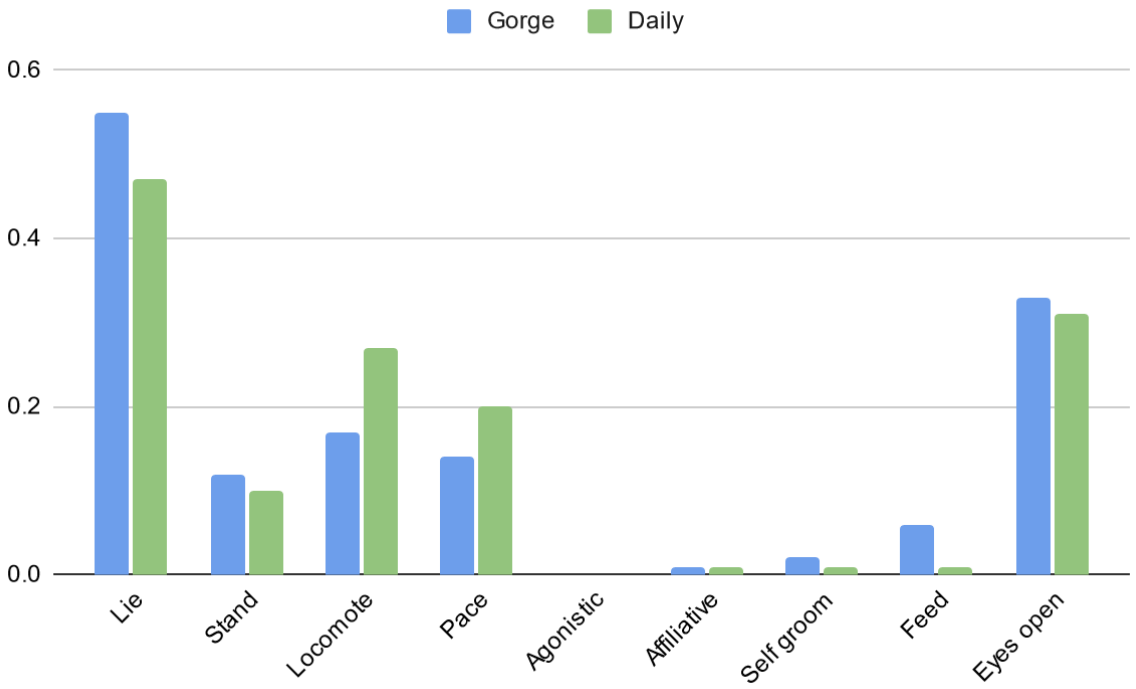

Fig 5. Average proportion of scans in which each behaviour was performed by the male and female adult tiger during gorge versus daily feeding.

Table 8. Chi-squared test results on number of scans in which the adult male and female tiger engaged in each behaviour during gorge feeding and daily feeding.

Behaviour	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
Lie	268	301	314	340	1223	0.10	0.750
Stand	74	495	64	590	1223	3.15	0.076
Locomote	119	450	178	476	1223	6.57	**0.010**
Pacing	100	19	130	48	297	4.94	**0.026**
Agonistic behaviour	1	568	1	653	1223	0.37	0.541
Affiliative behaviour	6	563	3	651	1223	0.78	0.379
Self-groom	10	559	7	647	1223	1.05	0.306
Feed	27	542	13	641	1223	7.31	**0.007**
Eyes open	166	403	202	452	1223	0.42	0.515
Lie with eyes open	153	115	196	118	582	1.71	0.191

When evaluated separately, it was clear that both the adult tigers (see Appendix Table 5 and Appendix Table 6 for individual differences) showed a significant difference in stereotypic pacing across feeding methods. Both the adult male and the adult female showed less pacing during gorge feeding.

3.3.1 Effect of feeding method on behaviour of the young tigers

Table 9 shows the results of the chi-squared tests comparing the behaviour of the three juvenile tiger cubs on the two feeding methods (see Appendix Table 7 for summary statistics). Significant differences were found in the number of scans when they were lying ($p=0.019$), locomoting overall ($p=0.010$), performing pacing locomotion specifically ($p=0.033$), feeding ($p<0.001$), and observed with eyes open ($p=0.048$). There was an increase in lying, locomoting and eyes open, and a tendency for more lying with eyes open specifically ($p=0.062$), and a decrease in feeding behaviour during daily feeding (Fig. 6). On an individual basis, the young female tiger (Appendix Table 8) was the only tiger showing a significant difference in lying with eyes open, which went from 38 % during gorge feeding to 56 % during daily feeding. The pacing for the individual young tigers did not differ between feeding routines (see Appendix Tables 8, 9 and 10 for results on each individual of the young tigers).

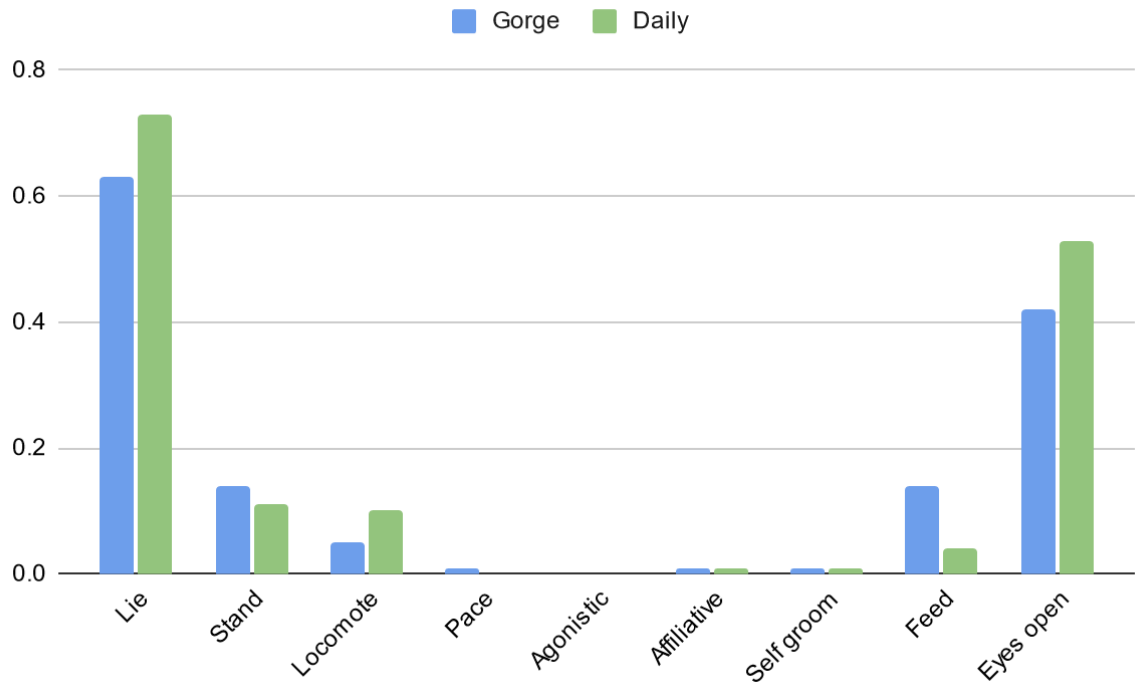

Fig 6. Average proportion of scans in which each behaviour was performed by the three young tigers during gorge versus daily feeding.

Table 9. Chi-squared test results on number of scans in which the juvenile tiger cubs (two males and one female) engaged in each behaviour during gorge feeding and daily feeding.

Behaviour	**Gorge feeding (Yes)**	**Gorge feeding (No)**	**Daily feeding (Yes)**	**Daily feeding (No)**	**Total (n scans)**	**Chi-squared**	**P-value**
Lie	564	294	695	286	1839	5.54	**0.019**
Stand	111	747	119	862	1839	0.27	0.602
Locomote	57	801	98	883	1839	6.64	**0.010**
Pacing	4	53	0	98	155	4.54	**0.033**
Agonistic behaviour	0	858	3	978	1839	1.09	0.297
Affiliative behaviour	15	843	12	969	1839	0.87	0.350
Self-groom	3	855	7	974	1839	0.55	0.459
Feed	102	756	49	932	1839	28.86	**<0.001**
Eyes open	395	463	497	484	1839	3.92	**0.048**
Lie with eyes open	369	195	489	206	1259	3.49	0.062

3.4 Effect of feeding method on use of space by the adult lions

The adult lions were seen significantly more often in the BR ($p<0.001$), PLAINS ($p<0.001$), STAIRS ($p=0.026$), TREES ($p<0.001$) areas during gorge feeding than daily feeding, and tended to use the DVW (0.059) more during gorge feeding. They were seen significantly more often in the PR ($p<0.001$), PRES ($p<0.001$), TOP ($p=0.043$), and UVA ($p<0.001$) areas during daily feeding (Fig. 7; Table 10; see Appendix Table 11 for proportions). When looking at the behaviour of the two lions separately, the male lion spent significantly more time (Appendix Table 12) in TREES ($p<0.001$) during gorge feeding, and significantly more time in BR ($p=0.005$), PR ($p<0.001$), PRES ($p=0.029$) and UVA ($p<0.001$) during daily feeding. The female lion (Appendix Table 13) spent significantly more time in BR ($p<0.001$) and PLAINS ($p=0.007$) during gorge feeding, and significantly more time in PR ($p<0.001$), PRES ($p<0.001$), TOP ($p<0.001$) and UVA ($p=0.002$) during daily feeding.

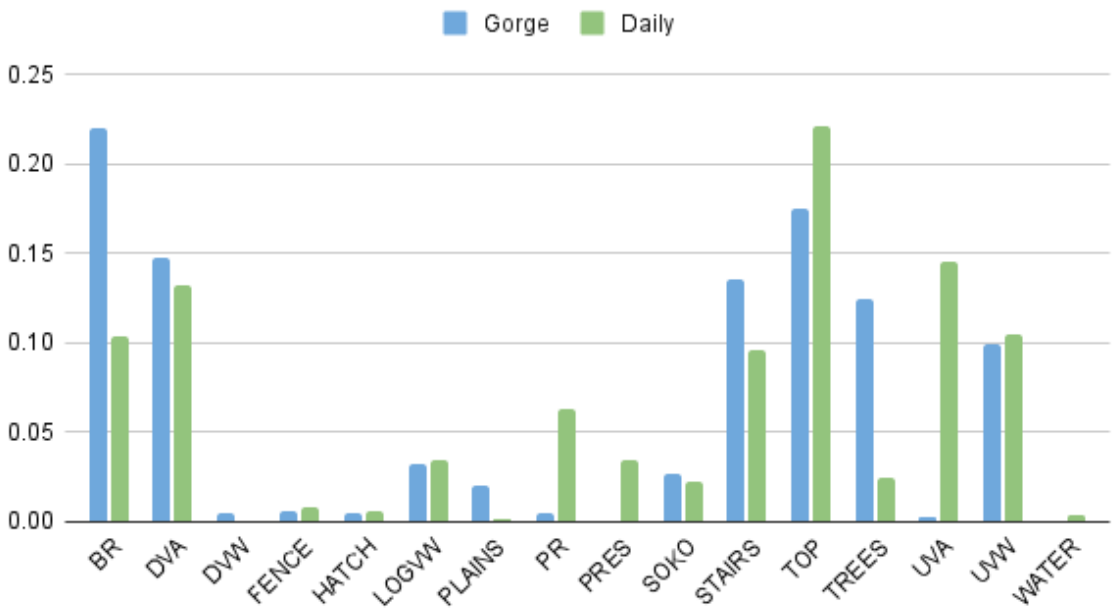

Fig 7. Average proportion of scans spent by the male and female adult lion in different locations of the enclosure during gorge- versus daily feeding. The code names are explained in Figs. 1 and 2.

Table 10. Chi-squared test results on number of scans in which the adult male and female lion were observed in different locations of the enclosure during gorge feeding and daily feeding. See Figs. 1-2 for location codes.

Location	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
BR	109	387	92	794	1382	34.38	**<0.001**
DVA	73	423	117	769	1382	0.61	0.434
DVW	2	494	0	886	1382	1.33	0.249
FENCE	3	493	7	879	1382	0.00	0.956
HATCH	2	494	5	881	1382	0	1
LOGVW	16	480	30	856	1382	0.02	0.873
PLAINS	10	486	1	885	1382	12.27	**<0.001**
PR	2	494	56	830	1382	27.69	**<0.001**
PRES	0	496	30	856	1382	17.16	**<0.001**
SOKO	13	483	20	866	1382	0.18	0.671
STAIRS	67	429	85	801	1382	4.97	**0.026**
TOP	87	409	196	690	1382	4.09	**0.043**
TREES	62	434	22	864	1382	55.89	**<0.001**
UVA	7	495	129	757	1382	76.92	**<0.001**
UVW	49	447	93	793	1382	0.13	0.717
WATER	0	496	3	883	1382	0.48	0.487

3.5 Effect of feeding method on use of space by the adult tigers

As seen in Fig. 8 and Table 11, the adult tigers spent more time in the BR area ($p<0.001$) during gorge feeding than daily feeding and tended to spend more time at the TOP ($p=0.073$) where the tigers were served their gorge meals. In contrast, they spent more time spent at PRES ($p<0.001$), ROCK ($p<0.001$), and WB ($p=0.021$) during daily feeding than gorge feeding. Appendix Table 14 provides the average proportion of scans in the different locations depending on the feeding method. Appendix Table 15 shows the statistics for the male tiger and Appendix Table 16 shows the statistics for the female tiger.

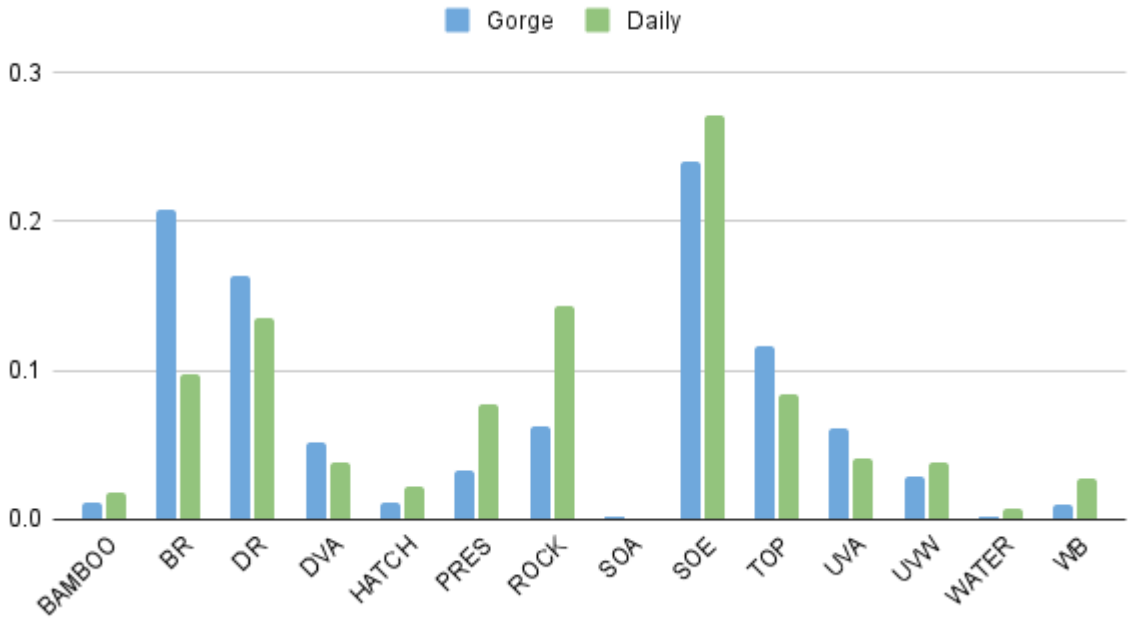

Fig 8. Average proportion of scans spent by the adult male and female tiger in different locations of the enclosure during gorge- versus daily feeding. The code names are explained in Fig. 1 and 3.

Table 11. Chi-squared test results on number of scans in which the adult male and female tiger were observed in different locations of the enclosure during gorge feeding and daily feeding. See Figs. 1 and 3 for location codes.

Location	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
BAMBOO	6	551	10	536	1103	1.09	0.295
BR	116	441	53	493	1103	26.27	**0.001**
DR	91	466	74	472	1103	1.68	0.195
DVA	29	528	21	525	1103	1.17	0.278
HATCH	6	551	12	534	1103	2.15	0.142
PRES	18	539	42	504	1103	10.66	**0.001**
ROCK	35	522	78	468	1103	19.20	**0.001**
SOA	1	558	0	546	1103	0	1
SOE	134	423	148	398	1103	1.34	0.246
TOP	65	492	46	500	1103	3.20	0.073
UVA	34	523	22	524	1103	2.46	0.117
UVW	16	541	21	525	1103	0.81	0.369
WATER	1	556	4	542	1103	0.84	0.358
WB	5	552	15	531	1103	5.30	**0.021**

3.6 Effect of feeding method on use of space by the young tigers

The young tigers showed many differences in use of their enclosure space between the two feeding methods. Fig. 9 shows that they spent more time at BR ($p<0.001$), SOE ($p<0.001$), and TOP ($p<0.001$) during gorge feeding than daily feeding. They also spent a bit more time at UVA ($p=0.042$) and UVW ($p<0.001$) during gorge feeding. During daily feeding, they spent more time in BAMBOO ($p<0.001$), DVA ($p<0.001$), HATCH ($p<0.001$), PRES ($p<0.001$), and ROCK ($p<0.001$) and a bit more time in WB ($p<0.001$; Table 12). Time at WATER was low but use of this feature tended to be higher during daily - than gorge feeding ($p=0.068$). Appendix Table 14 shows the average proportion of scans in the different locations depending on the feeding method. Appendix Tables 17 - 19 show the individual young tigers' statistics.

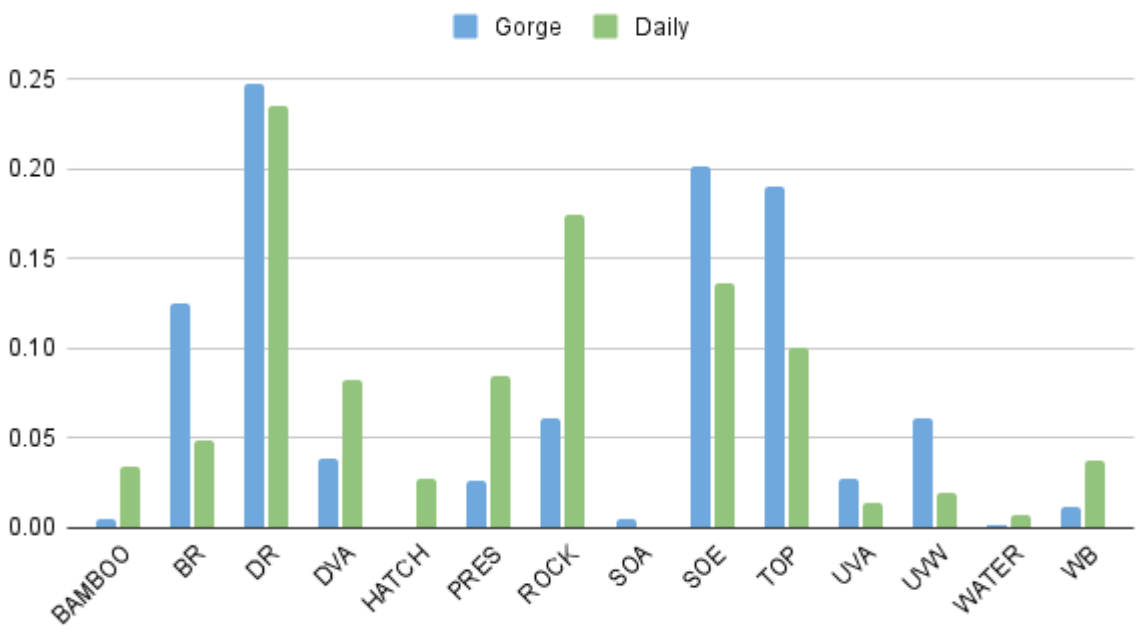

Fig 9. Average proportion of scans spent by the three young tigers in different locations of the enclosure during gorge- versus daily feeding. The code names are explained in Figs. 1 and 3.

Table 12. Chi-squared test results on number of scans in which the three young tigers were observed in different locations of the enclosure during gorge feeding and daily feeding. See Figs. 1 and 3 for location codes.

Location	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
BAMBOO	4	838	30	857	1729	18.93	**<0.001**
BR	105	737	43	844	1729	32.06	**<0.001**
DR	209	633	209	678	1729	0.37	0.541
DVA	32	810	73	814	1729	14.85	**<0.001**
HATCH	0	842	24	863	1729	23.10	**<0.001**
PRES	22	820	75	812	1729	27.84	**<0.001**
ROCK	51	791	155	732	1729	53.65	**<0.001**
SOA	4	838	0	887	1729	2.42	**0.120**
SOE	170	672	121	766	1729	13.23	**<0.001**
TOP	160	682	89	798	1729	28.18	**<0.001**
UVA	23	819	12	875	1729	4.13	**0.042**
UVW	51	791	17	870	1729	19.60	**<0.001**
WATER	1	841	6	881	1729	2.10	0.148
WB	10	832	33	854	1729	11.42	**<0.001**

4. Discussion

In this study, I expected that, when gorge fed, both lions and tigers would exhibit less stereotypic pacing, agonistic behaviour, lying awake with eyes open (vs sleeping), and self-grooming while performing more standing, non-stereotyped locomotion, feeding, and affiliative behaviour compared to when they received daily feeding. I also expected that their use of enclosure space would vary between the feeding methods, with gorge feeding leading to more roaming over the whole enclosure instead of staying near the feeding area. The results showed that the feeding methods affected the behaviour and use of space of both the lions and the tigers. Different settings and factors could play a big role in affecting the animals' behaviour from day to day which are important to shine a light on when going through the results of this study.

The chi-squared results on stereotyped pacing suggest that, for the male and female lions' combined results, their behaviour was more natural on gorge feeding than daily feeding. Looking at the individual results, the female lion paced less during gorge feeding, but the male lion seemed to pace at similar levels during both feeding methods. The young tigers did

not differ between the feeding routines on the levels on pacing when looking at them individually. However, the combined results for the adult tigers showed that gorge-feeding reduced pacing, and seeing the individual results gorge feeding was benefited by both. There might be a few reasons for this. This might indicate that the gorge feeding routine is better suited for the tigers in this situation, or that the male lion didn't adapt to the feeding routines as quickly as the tigers. It is usual for pacing to increase in older captive big cats (Mohapatra et al., 2014), explaining higher levels in both the adult lions and tigers compared to the young tigers. For the tigers, feeding behaviour was higher during gorge feeding than daily feeding, probably because they had access to the scraps or carcass for several days after feeding during gorge feeding. The lions tended to show more feeding during gorge feeding but this was not statistically significant. The tigers were only gorge-fed once a week whereas the lions were gorge-fed twice a week. This could explain why the adult tigers benefited more from the gorge-feeding than the adult male lion. It is possible that differences in the feeding habits of lions and tigers in nature could explain differences in how they responded to the gorge feeding in captivity. Tigers may be better adapted to long intervals between meals than lions. For example, Sunquist (2010) reported that wild tigers typically eat one large prey per week while Schaller (1972) observed wild lions feeding once every 2.5 to 3.5 days. Lions are also known to steal the prey of other species, which is possible when the pride cooperates to overpower hyenas and smaller predators at their kills (Schaller, 1972; Watts and Holekamp, 2008). This behaviour may allow them to feed more frequently than tigers. Reasons for differences between the individual adults could be because the adult female lion was still nursing cubs, and the female tiger was in heat during the observations.

Lying with eyes open was evaluated because this behaviour may indicate boredom (Burn, 2017). The adult lions, and the young female tiger, showed more of this behaviour during daily feeding than during gorge feeding, which can be because of the expectation of food and because they're waiting to be fed. It might also just be because they were observing people or animals in nearby enclosures. Imagining the animals were more content and satisfied after gorge meals, they might sleep more when lying instead of lying awake.

The pacing seen on gorge days might be because of the expectation of food. If the animals aren't used to this feeding method, but a daily feeding routine, the expectation of food might have been stressful for the animals (Mellen and Shepherdson, 1997), causing them to spend time on pacing. The length of this study might have been too short for the animals to settle

with one feeding routine. It could have been longer to make sure the animals were really used to gorge feeding upon the start of the study. If the animals are used to getting fed every day (approximately), days with no meal during gorge feeding may make them stressed because of the expectation of getting fed the next day. In the gorge feeding, the animals could feel full and satisfied for a longer period and become hungry towards the end of gorge feeding, when the time for wanting a new meal approached. Fewer observations were made during gorge feeding than daily feeding, and variation in the number of observations of each animal at the times when that animal was most likely to be pacing could have affected the results. In the study by Finch et al. (2020), the lions were apparently more satisfied by a more natural feeding schedule with large meals, and stereotypical behaviour like pacing decreased with this method. Resting also increased after a large meal in that study.

The main cause of pacing in the lions at Dyreparken might be because of expectation. It is also possible that some of the pacing seen in the male lion in the outdoor enclosure could have been patrolling, which is a natural behaviour for male lions as they patrol their territory in the wild (Lehmann, 2007). There was also limited space for both the animal groups compared to what they would use in nature, where both lions and tigers use much greater areas and often travel for long distances (Funston et al., 2003). Lack of access to large amounts of space could have contributed to boredom or stress in the animals, causing them to develop a pacing stereotypy over time. If some of the locomotion along the fence line of the outdoor enclosure by the male lion was patrolling and not pacing, the pacing happened mostly in the indoor area. This was more clear repetitive pacing and might have been stimulated by expectation of getting let outside into the outdoor enclosure or a lack of stimuli that would lead the animals to take varied pathways when locomoting (Clubb and Mason, 2003; Clubb and Mason, 2007; Harper et al., 2016). Pacing often happened before the lions were let outside in the mornings, or if the lions had to stay inside for the day, which happened on some days because of maintenance in the outdoor enclosure.

Generally, the pacing behaviour was most common in the adult males of both species. The adult male tiger always showed a lot of pacing during almost all the observations, and the male lion was also showing a lot of pacing during this (which could have been patrolling in some cases). We know the male tiger came from a smaller zoo, and I was told by the zookeepers that he had a history of pacing before coming to Dyreparken. The pacing could then have been a matter of a strong habit that would be hard to stop completely even if the

environmental conditions were better at Dyreparken, and gorge feeding clearly reduced his pacing compared to daily feeding. There was hardly any pacing seen in the young tigers. This could be because they were born in at Dyreparken, where they had a relatively spacious and varied outdoor habitat.

Other behaviours that were predicted to show significant differences between feeding methods were agonistic behaviour, self-grooming, performing more standing and affiliative behaviour, and it was predicted that the lions and tigers would exhibit these behaviours less during gorge feeding. Results showed there weren't any significant differences in these behaviours for any of the animals. The reason that the lions and tigers didn't show more agonistic behaviour during gorge feeding or daily feeding could be because of the group dynamics already being settled, and there was no need for agonistic behaviour even if this was predicted to increase during gorge feeding because of the possibility of fighting over food. Self-grooming did not show significant differences between the feeding methods which could be because it was also rarely recorded for both species. It was predicted that self-grooming would increase during daily feeding, as it is a behaviour that can be performed when bored (Burn, 2017). Standing was another behaviour that didn't differ significantly from the two feeding methods, as well as the affiliative behaviour, even if these behaviours were predicted to increase during gorge feeding. Affiliative behaviour was rarely recorded for both lions and tigers and did not show any significant differences between feeding methods. Seeing as tigers are solitary animals it might not come naturally for them, even if affiliative behaviour has been recorded in captive tiger groups in earlier studies (Holland, 2023). If the adult female tiger was expected to show affiliative behaviour towards her female cub, and as well as her two male cubs (if they weren't separated during the study) though less than usual because she was in heat. Tiger cubs in nature stay with their mother for 2-3 years before leaving to establish own territory, and to learn how to become good hunters. Before this, they rely on their mother to bring them prey (Sunquist and Sunquist, 2014; Miquelle et al., 2010). If she weren't separated from the male during the study, she might have been observed showing more affiliative behaviour towards the adult male because she was in heat.

The feeding methods caused changes in how the animals used the enclosure space. However, it was not clear that they roamed further on days with one method of feeding versus the other method. They were seen to use all areas of the enclosures during both feeding methods, only

with a few exceptions. The reason for this might have been because of a few factors like following their cubs around in the outdoor enclosure when the cubs were let outside for the first time Another reason could be their outdoor enclosure being closed off to access for the lions for a few days before the lion cubs was let outside for the first time (which was closer to the end of the study), to prepare the enclosure and to make sure it was safe for the cubs. This could've caused them to explore and use more of their indoor area. The tigers tended to stay around the area they were fed a lot more in the outdoor enclosure during gorge feeding which could be because the carcass was left there after feeding time, and the tigers were observed feeding on this for several days. Another reason that could affect the space use could be the tigers were switched from being in the outdoor enclosure to the indoor area with the small outdoor enclosure about every other day.

Weather also seemed to affect the animals, especially the adult lioness. The male lion was not affected by bad weather to the same level as the lioness, and this might be because of the big mane that can provide with some extra insulation and protection (Shea, 2013). The lioness tended to stay inside while the male lion went outside in the rain and the cold. The lions also had four cubs which might have caused the lioness to stay inside more as females are very protective of their offspring (Shea, 2013), but she did go outside on some nice sunny days and tended to show lots of energy and playfulness on those days. The cubs were too young to go outside in the winter weather, but they were allowed to explore the outside for the first time a few days before the end of the study. This could have caused the lions to be more active or stressed at this time, especially the male lion who was very active during this time. Apart from the cubs being let out, the large number of people visiting the zoo at this time could have contributed to his higher activity. A male lion is very protective of his pride, including his cubs, which could have increased patrolling by the male lion to mark his territory, which could then have been misinterpreted as pacing (Lehmann, 2007).

The study was mostly conducted in the low season for the zoo, which affected the number of people visiting the zoo. People could affect the behaviour of the animals, and if many people were present, this might cause more stimulation or stress (Wielebnowski, 2003). The last week of the study coincided with the Norwegian winter holiday, which caused a sudden large increase in the number of zoo visitors, from barely any people to a very full zoo. This could possibly have caused the animals to be more active or stressed at this time.

Some further factors should be taken into consideration as well when looking at the results. For example, on some days some animals were out of sight for long periods which could last for an entire observation day. This created “holes” in the data. The female tiger was out of sight for long periods because she was separated from the rest of the tigers due to being in heat. On some occasions, it was impossible to find her either in person and via the cameras. The cameras did not cover all the places where animals could hide, making it unclear what they were doing at certain times. The number of observations, and behaviour observed, also varied due to presentations of the animals to the public on some days.

5. Conclusions

Taking all the results of this study into consideration, the conclusion is that the two different feeding routines made a difference to behaviour and use of enclosure space in both species. The pacing by both adult tigers occurred more frequently during daily feeding whereas it differed more in the female lion than the male lion, and it was the lioness that showed less occurrence of pacing during gorge feeding. Therefore, gorge feeding appeared to have a better effect on the adult tigers than the male lion, especially the adult male tiger by reducing stereotypical pacing, and the juvenile female tiger by reducing lying with eyes open. The gorge feeding also increased time spent feeding, especially in the tigers, which suggests that it was positive for encouraging natural behaviour and providing enrichment. Seeing as this study was very short and the animals had little time to adjust to the different feeding routines, it is recommended that future studies on gorge feeding are conducted over several months to ensure that the results are based on animals that have become used to being fed this way. Further studies on the effects of different feeding routines in lions and tigers in a zoo environment should be made to determine how to secure the best possible welfare for big cats kept in zoos.

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7. Appendix

Appendix Table 1. Summary statistics on the proportion of scans engaged in different behaviours by the male and female adult lion during the gorge and daily feeding periods.

Feeding method	Days since eating	Temper-ature (C)	Visi-tors (n)	Lie	Stand	Loco-mote	Pace	Agonis-tic	Affil-iative	Self-groom	Feed	Eyes open
Gorge												
Observa-tions (n)	18	18	18	18	18	18	18	18	18	18	18	18
Average	2.78	2.64	5.99	0.60	0.11	0.22	0.14	0.01	0.03	0.02	0.04	0.26
SD	1.35	2.87	7.01	0.27	0.09	0.19	0.12	0.01	0.03	0.05	0.07	0.15
Max-Value	5.00	6.75	19.00	1.00	0.30	0.63	0.30	0.03	0.10	0.20	0.23	0.53
Min-Value	1.00	-1.33	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Daily												
Observa-tions (n)	28	14	14	14	14	14	14	14	14	14	14	14
Average	1.00	3.31	11.06	0.63	0.14	0.23	0.06	0.00	0.03	0.02	0.01	0.41
SD	0.00	1.81	9.74	0.18	0.09	0.10	0.07	0.01	0.02	0.03	0.03	0.13
Max-Value	1.00	7.00	37.18	0.83	0.33	0.44	0.18	0.03	0.07	0.10	0.13	0.71
Min-Value	1.00	0.67	0.00	0.26	0.03	0.10	0.00	0.00	0.00	0.00	0.00	0.23

Appendix Table 2. Chi-squared test results on number of scans in which the adult male lion engaged in each behaviour during gorge feeding and daily feeding.

Behaviour	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
Lie	163	100	291	36	590	59.97	**<0.001**
Stand	20	243	52	275	590	9.37	**0.002**
Locomote	52	211	114	213	590	16.42	**<0.001**
Pacing	17	35	38	76	166	0.01	0.933
Agonistic behaviour	3	260	2	325	590	0.06	0.806
Affiliative behaviour	6	257	5	322	590	0.13	0.715
Self-groom	1	262	2	325	590	0.04	0.850
Feed	15	248	15	312	590	0.38	0.540
Eyes open	75	188	165	162	590	29.08	**<0.001**
Lie with eyes open	73	90	161	130	454	4.65	**0.031**

Appendix Table 3. Chi-squared test results on number of scans in which the adult female lion engaged in each behaviour during gorge feeding and daily feeding.

Behaviour	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
Lie	142	121	290	175	728	4.88	**0.027**
Stand	40	223	66	399	728	0.14	0.709
Locomote	63	200	106	359	728	0.13	0.722
Pacing	24	39	77	29	169	19.61	**<0.001**
Agonistic behaviour	1	262	1	464	728	0.11	0.742
Affiliative behaviour	11	252	15	450	728	0.45	0.504
Self-groom	7	256	8	457	728	0.74	0.391
Feed	7	256	5	460	728	1.72	0.190
Eyes open	76	187	183	282	728	8.02	**0.005**
Lie with eyes open	71	71	176	114	432	4.45	**0.035**

Appendix Table 4. Summary statistics on the proportion of scans engaged in different behaviours by the male and female adult tiger during the gorge and daily feeding periods.

Feeding method	Days since eating	Temperature (C)	Visitors (n)	Lie	Stand	Locomote	Pace	Agonistic	Affiliative	Self-groom	Feed	Eyes open
Gorge												
Observations (n)	16	16	16	16	16	16	16	16	16	16	16	16
Average	1.91	2.52	5.87	0.55	0.12	0.17	0.14	0.00	0.01	0.02	0.06	0.33
SD	0.83	3.00	8.17	0.29	0.11	0.16	0.14	0.01	0.02	0.03	0.11	0.22
Max-Value	3.00	7.72	20.67	1.00	0.35	0.42	0.39	0.03	0.05	0.10	0.30	0.75
Min-Value	1.00	-1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Daily												
Observations (n)	28	28	28	28	28	28	28	28	28	28	28	28
Average	0.93	3.70	10.54	0.47	0.10	0.27	0.20	0.00	0.01	0.01	0.01	0.31
SD	0.26	1.35	6.93	0.22	0.08	0.23	0.22	0.01	0.01	0.02	0.04	0.18
Max-Value	1.00	6.50	23.33	0.95	0.31	0.77	0.63	0.03	0.05	0.07	0.17	0.70
Min-Value	0.00	1.67	1.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix Table 5. Chi-squared test results on number of scans in which the adult male tiger engaged in each behaviour during gorge feeding and daily feeding.

Behaviour	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
Lie	134	149	122	205	610	6.28	**0.012**
Stand	40	243	32	295	610	2.76	0.097
Locomote	89	194	151	176	610	13.79	**<0.001**
Pacing	7	82	128	23	240	134.56	**<0.001**
Agonistic behaviour	1	282	1	326	610	0.37	0.544
Affiliative behaviour	3	280	2	325	610	0.03	0.872
Self-groom	7	276	6	321	610	0.30	0.586
Feed	16	267	4	323	610	9.39	**0.002**
Eyes open	76	207	73	254	610	1.69	0.194
Lie with eyes open	67	67	69	53	256	1.10	0.294

Appendix Table 6. Chi-squared test results on number of scans in which the adult female tiger engaged in each behaviour during gorge feeding and daily feeding.

Behaviour	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
Lie	134	152	192	135	613	8.62	**0.003**
Stand	34	252	32	295	613	0.70	0.402
Locomote	30	256	27	300	613	0.90	0.342
Pacing	12	18	25	2	57	17.25	**<0.001**
Agonistic behaviour	0	286	0	327	613	0.00	0.964
Affiliative behaviour	3	283	1	326	613	0.41	0.524
Self-groom	3	283	1	326	613	0.41	0.524
Feed	11	275	9	318	613	0.58	0.447
Eyes open	90	196	129	198	613	4.23	**0.040**
Lie with eyes open	86	48	127	65	326	0.13	0.714

Appendix Table 7. Summary statistics on the proportion of scans engaged in different behaviours by the young tigers (one female and two males) during the gorge and daily feeding periods.

Feeding method	Days since eating	Tempera-ture (C)	Visitors (n)	Lie	Stand	Loco-mote	Pace	Agonis-tic	Affilia-tive	Self-groom	Feed	Eyes open
Gorge												
Observations (n)	24	24	24	24	24	24	24	24	24	24	24	24
Average	1.80	2.67	5.81	0.63	0.14	0.05	0.01	0.00	0.01	0.01	0.14	0.42
SD	0.77	2.91	8.12	0.26	0.12	0.05	0.01	0.00	0.02	0.02	0.16	0.19
Max-Value	3.00	7.72	20.67	1.00	0.37	0.16	0.03	0.00	0.07	0.10	0.45	0.85
Min-Value	1.00	-1.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Daily												
Observations (n)	42	42	42	42	42	42	42	42	42	42	42	42
Average	0.93	3.70	10.54	0.73	0.11	0.10	0.00	0.00	0.01	0.01	0.04	0.53
SD	0.26	1.34	6.89	0.17	0.09	0.09	0.00	0.01	0.02	0.01	0.08	0.18
Max-Value	1.00	6.50	23.33	1.00	0.30	0.37	0.00	0.07	0.08	0.07	0.37	0.90
Min-Value	0.00	1.67	1.67	0.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13

Appendix Table 8. Chi-squared test results on number of scans in which the young female tiger engaged in each behaviour during gorge feeding and daily feeding.

Behaviour	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
Lie	166	120	229	98	613	9.57	**0.002**
Stand	33	253	41	286	613	0.14	0.705
Locomote	24	262	30	297	613	0.12	0.733
Pacing	2	22	0	30	54	0.78	0.376
Agonistic behaviour	0	286	2	325	613	0.38	0.539
Affiliative behaviour	5	281	5	322	613	0.01	0.916
Self-groom	0	286	2	325	613	0.38	0.539
Feed	27	259	15	312	613	5.63	**0.018**
Eyes open	121	165	175	152	613	7.68	**0.006**
Lie with eyes open	116	50	171	58	395	1.11	0.292

Appendix Table 9. Chi-squared test results on number of scans in which one young male tiger (U1) engaged in each behaviour during gorge feeding and daily feeding.

Behaviour	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
Lie	200	86	237	90	613	0.48	0.487
Stand	40	246	37	290	613	0.99	0.319
Locomote	16	270	33	294	613	4.20	**0.041**
Pacing	1	15	0	33	49	0.14	0.708
Agonistic behaviour	0	286	0	327	613	0.00	0.964
Affiliative behaviour	4	282	4	323	613	0.03	0.869
Self-groom	3	283	3	324	613	0.06	0.805
Feed	30	256	14	313	613	8.83	**0.003**
Eyes open	145	141	179	148	613	1.00	0.317
Lie with eyes open	131	69	178	59	437	4.83	**0.028**

Appendix Table 10. Chi-squared test results on number of scans in which the second young male tiger (U2) engaged in each behaviour during gorge feeding and daily feeding.

Behaviour	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
Lie	198	88	229	98	613	0.05	0.830
Stand	38	248	41	286	613	0.08	0.783
Locomote	17	269	35	292	613	4.45	**0.035**
Pacing	1	16	0	35	52	0.14	0.709
Agonistic behaviour	0	286	1	326	613	0.01	0.944
Affiliative behaviour	6	280	3	324	613	0.77	0.381
Self-groom	0	286	2	325	613	1.75	0.185
Feed	45	241	20	307	613	14.89	**<0.001**
Eyes open	129	157	143	184	613	0.12	0.733
Lie with eyes open	122	76	140	89	427	0.01	0.919

Appendix Table 11. Average proportion of scans in which the adult male and female lion were seen in different locations of their enclosure during gorge feeding and daily feeding. Location codes are shown in Fig. 1-2.

	Lions	
Location	Gorge	Daily
BR	0.22	0.10
DVA	0.15	0.13
DVW	0.00	0.00
FENCE	0.01	0.01
HATCH	0.00	0.01
LOGVW	0.03	0.03
PLAINS	0.02	0.00
PR	0.00	0.06
PRES	0.00	0.03
SOKO	0.03	0.02
STAIRS	0.14	0.10
TOP	0.18	0.22
TREES	0.13	0.02
UVA	0.00	0.15
UVW	0.10	0.10
WATER	0.00	0.00

Appendix Table 12. Chi-squared test results on number of scans in which the adult male lion Iwas observed in different locations of the enclosure during gorge feeding and daily feeding. See Figs. 1-2 for location codes.

Location	**Gorge feeding (Yes)**	**Gorge feeding (No)**	**Daily feeding (Yes)**	**Daily feeding (No)**	**Total (n scans)**	**Chi-squared**	**P-value**
BR	55	180	62	361	658	7.91	**0.005**
DVA	23	212	29	394	658	1.78	0.182
DVW	0	235	0	423	658	0.00	0.964
FENCE	3	232	4	419	658	0	1
HATCH	0	235	1	422	658	0.09	0.765
LOGVW	3	232	13	410	658	2.06	0.152
PLAINS	3	232	0	423	658	2.98	0.084
PR	0	235	18	405	658	10.28	**<0.001**
PRES	0	235	11	412	658	4.73	**0.029**
SOKO	6	229	7	416	658	0.25	0.616
STAIRS	6	229	3	420	658	2.56	0.109
TOP	77	158	127	296	658	0.53	0.466
TREES	41	194	1	422	658	74.88	**<0.001**
UVA	0	235	108	315	658	71.78	**<0.001**
UVW	18	217	39	384	658	0.46	0.495
WATER	0	235	0	423	658	0.00	0.964

Appendix Table 13. Chi-squared test results on number of scans in which the adult female lion was observed in different locations of the enclosure during gorge feeding and daily feeding. See Figs. 1-2 for location codes.

Location	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
BR	54	207	30	433	724	32.86	**<0.001**
DVA	50	211	88	375	724	0.00	0.960
DVW	2	259	0	463	724	1.32	0.251
FENCE	0	261	3	460	724	0.49	0.483
HATCH	2	259	4	459	724	0.08	0.773
LOGVW	13	248	17	446	724	0.72	0.396
PLAINS	7	254	1	462	724	7.17	**0.007**
PR	2	259	38	425	724	17.71	**<0.001**
PRES	0	261	19	444	724	11.00	**<0.001**
SOKO	7	254	13	450	724	0.01	0.921
STAIRS	61	200	82	381	724	3.37	0.066
TOP	10	251	69	394	724	21.05	**<0.001**
TREES	21	240	21	442	724	3.76	0.052
UVA	1	260	21	442	724	9.77	**0.002**
UVW	31	230	54	409	724	0.01	0.931
WATER	0	261	3	460	724	0.49	0.483

Appendix Table 14. Average proportion of scans in which the adult male and female tiger, and the juvenile tiger cubs, were seen in different locations of their enclosure during gorge feeding and daily feeding. Location codes are shown in Fig. 1-2.

	Adult tigers		Tiger Cubs	
Location	Gorge	Daily	Gorge	Daily
BAMBOO	0.01	0.02	0	0.03
BR	0.21	0.10	0.12	0.05
DR	0.16	0.14	0.25	0.24
DVA	0.05	0.04	0.04	0.08
HATCH	0.01	0.02	0	0.03
PRES	0.03	0.08	0.03	0.08
ROCK	0.06	0.14	0.06	0.17
SOA	0	0	0	0
SOE	0.24	0.27	0.2	0.14
TOP	0.12	0.08	0.19	0.10
UVA	0.06	0.04	0.03	0.01
UVW	0.03	0.04	0.06	0.02
WATER	0	0.01	0	0.01
WB	0.01	0.03	0.01	0.04

Appendix Table 15. Chi-squared test results on number of scans in which the adult male tiger was observed in different locations of the enclosure during gorge feeding and daily feeding. See Figs. 1 and 3 for location codes.

Location	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
BAM-BOO	5	280	10	285	580	1.54	0.215
BR	25	260	25	270	580	0.02	0.899
DR	77	208	73	222	580	0.39	0.532
DVA	13	272	4	291	580	5.24	**0.022**
HATCH	0	285	8	287	580	5.97	**0.014**
PRES	6	279	29	266	580	15.26	**<0.001**
ROCK	7	278	26	269	580	10.92	**<0.001**
SOA	1	284	0	295	580	0	1
SOE	78	207	47	248	580	11.21	**<0.001**
TOP	48	237	38	257	580	1.80	0.180
UVA	18	267	11	284	580	2.04	0.153
UVW	3	282	12	283	580	5.23	**0.022**
WATER	0	285	4	291	580	2.16	0.141
WB	4	281	8	287	580	1.22	0.268

Appendix Table 16. Chi-squared test results on number of scans in which the adult female tiger was observed in different locations of the enclosure during gorge feeding and daily feeding. See Figs. 1 and 3 for location codes.

Location	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
BAM-BOO	1	271	0	251	523	0.00	0.964
BR	91	181	28	223	523	36.94	**<0.001**
DR	14	258	1	250	523	10.57	**<0.001**
DVA	16	256	17	234	523	0.18	0.676
HATCH	6	266	4	247	523	0.04	0.847
PRES	12	260	13	238	523	0.17	0.681
ROCK	28	244	52	199	523	10.95	**<0.001**
SOA	0	272	0	251	523	0.00	0.964
SOE	56	216	101	150	523	24.00	**<0.001**
TOP	17	255	8	243	523	2.69	0.101
UVA	16	256	11	240	523	0.60	0.439
UVW	13	259	9	242	523	0.46	0.497
WATER	1	271	0	251	523	0.00	0.964
WB	1	271	7	244	523	3.6	0.058

Appendix Table 17. Chi-squared test results on number of scans in which the young female tiger was observed in different locations of the enclosure during gorge feeding and daily feeding. See Figs. 1 and 3 for location codes.

Location	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
BAMBOO	3	272	11	286	572	4.08	**0.043**
BR	53	222	14	283	572	29.27	**<0.001**
DR	57	218	73	224	572	1.21	0.272
DVA	10	265	21	276	572	3.29	0.070
HATCH	0	275	3	294	572	1.19	0.275
PRES	11	264	31	266	572	8.70	**0.003**
ROCK	19	256	67	230	572	27.38	**<0.001**
SOA	0	275	0	297	572	0.00	0.964
SOE	35	240	31	266	572	0.73	0.392
TOP	75	200	32	265	572	25.56	**<0.001**
UVA	3	272	1	296	572	0.34	0.562
UVW	5	270	1	296	572	1.76	0.184
WATER	1	274	1	296	572	0.43	0.513
WB	3	272	11	286	572	4.08	**<0.043**

Appendix Table 18. Chi-squared test results on number of scans in which one young male tiger (U1) was observed in different locations of the enclosure during gorge feeding and daily feeding. See Figs. 1 and 3 for location codes.

Location	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
BAMBOO	0	285	9	285	579	6.98	**0.008**
BR	22	263	11	283	579	4.26	**0.039**
DR	83	202	71	223	579	1.83	0.176
DVA	13	272	3	291	579	6.75	**0.009**
HATCH	0	285	7	287	579	5.02	**0.025**
PRES	4	281	21	273	579	11.54	**<0.001**
ROCK	10	275	32	262	579	11.70	**<0.001**
SOA	2	283	0	294	579	0.53	0.465
SOE	65	220	60	234	579	0.49	0.483
TOP	43	242	41	253	579	0.15	0.696
UVA	10	275	10	284	579	0.01	0.944
UVW	27	258	16	278	579	3.42	0.064
WATER	0	285	2	292	579	0.47	0.493
WB	6	279	11	283	579	1.36	0.244

Appendix Table 19. Chi-squared test results on number of scans in which the second young male tiger (U2) was observed in different locations of the enclosure during gorge feeding and daily feeding. See Figs. 1 and 3 for location codes.

Location	Gorge feeding (Yes)	Gorge feeding (No)	Daily feeding (Yes)	Daily feeding (No)	Total (n scans)	Chi-squared	P-value
BAM-BOO	1	281	10	286	578	7.07	**0.008**
BR	30	252	18	278	578	3.94	**0.047**
DR	69	213	65	231	578	0.51	0.475
DVA	9	273	49	247	578	28.56	**<0.001**
HATCH	0	282	14	282	578	13.67	**<0.001**
PRES	7	275	23	273	578	8.21	**0.004**
ROCK	22	260	56	240	578	15.29	**<0.001**
SOA	2	280	0	296	578	0.55	0.458
SOE	70	212	30	266	578	21.77	**<0.001**
TOP	42	240	16	280	578	14.40	**<0.001**
UVA	10	272	1	295	578	7.96	**0.005**
UVW	19	263	0	296	578	20.62	**<0.001**
WATER	0	282	3	293	578	1.25	0.265
WB	1	281	11	285	578	8.03	**0.005**

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