DID THE PANDEMIC LOCKDOWNS AFFECT THE WELFARE OF THE SUMATRAN ORANGUTANS (*Pongo abelii*) AT THE TORONTO ZOO?

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Abstract

The COVID-19 pandemic led to unprecedented lockdowns with rippling impacts on the lives of humans and animals alike. Fortunately, these lockdowns also presented the opportunity to study the relationship of visitor presence with the welfare of zoo-housed animals as natural experiments. The reduction of visitor counts to zero for several consecutive months allowed researchers to study visitor effects on welfare measures and address the confounding variables associated with the time of the day. The purpose of this thesis was to study how the welfare measures of the Toronto Zoo Sumatran orangutans (*Pongo abelii*) changed when visitors were reintroduced after the lockdowns were lifted. I compared behavioural and physiological measures of stress between the lockdown and visitor introduction phases. Specifically, I studied changes in aversive behaviour by measuring the equality of physical enclosure space use, as well as changes in behavioural indicators of arousal (self-directed behaviours, agonistic behaviours, and object-directed displacement) and a physiological indicator of arousal (fecal consistency) as visitors were reintroduced to the orangutan pavilion. I found that the orangutans did not change their space use when visitors were introduced. In fact, the orangutans hid less when visitors were introduced than during the lockdown. This suggests that visitor presence was not aversive to these orangutans. Foraging and inactivity levels did not change across the phases of the study. Behavioural indicators of arousal also did not change when visitors were introduced. Fecal consistency did not change across the study. However, the presence of conspecifics and keepers strongly affected the behaviours of the orangutans. The results are congruent with studies that found that the pandemic lockdown measures did not negatively affect the welfare of a variety of species.

Keywords: Welfare, Visitor effects, Stress, COVID-19, Lockdowns, Sumatran orangutan, Zoos

Dedication

This thesis is dedicated to my mother, Marie Anne F. Gading. I didn’t know what strength was until she showed me how to face adversity with a smile.

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1. Introduction

Human and non-human primate lives are inextricably linked with each other. As an order, primates, including humans, occupy almost every continent on the planet so there is a great deal of overlap and interaction between human and non-human primates (primates from herein). Thus, they affect each other's physical and psychological lives profoundly. Historically, the role of human influence on primate behaviour has been ignored in scientific studies. The scientific focus has slowly shifted towards the reciprocal role of humans and primates in shaping each other's customs and practices; and with that the understanding of human-primate interaction (Fuentes, 2012). Human density and behaviour vary when humans interact with free-ranging primates (Hosey, 2005). These interactions do not just happen deep in the jungles. In fact, studies have documented and explored the behaviours of primates in areas where humans are found in high density (Hosey, 2005) as in the case of urban or semi-free-ranging macaques and their interactions with tourists (*Macaca sylvanus*: Fa, 1992), surrounding temples in Bali (*Macaca fascicularis*: Small, 1998), and even among macaques who beg for food and live within towns in India (*Macaca mulatta*: Southwick & Siddiqi; 1998).

Meanwhile, as primate habitats are destroyed, primates are also increasingly living in captive settings, under human care. While opportunities for interaction between humans and primates in the wild are undeniable, captivity is unique in that the survival and agency of the animal is completely dependent on the space and management that humans provide (Hosey, 2005). Furthermore, encounters with humans are more protracted and often inescapable in human care than in the wild (Hosey, 2005). At least in accredited North American and European zoos, zoos are places where primates and humans affect each other's behaviours and lives (Patrick & Caplow, 2018; Safina, 2018). Humans influence zoo-housed primates' lives through management, provision of needs, and daily interaction (Hosey, 2005). Simarly, zoos allow space for primates to influence visitors' lives, behaviours, and cognition – especially towards nature. In mega-cities, humans are increasingly becoming apathetic towards nature because their existence has become removed from experiences with wild animals (Safina, 2018). Especially for people who cannot afford to fly to 'wild' habitats, zoos have become a place where humans connect with 'wild' animals (Safina, 2018). With the current focus of zoos on conservation, primates perform a critical role in education as ambassadors primarily because of their attractiveness to visitors (Carr, 2016; Patrick & Caplow, 2018; Whitworth, 2012). Additionally, valuable research in ethology and comparative cognition has been conducted on zoo-housed primates for behaviours that otherwise would have normally been missed in the

wild due to difficulty in observations (Hosey, 2005; MacDonald & Ritvo, 2016). As much as humans influence zoo-housed primate agency, primates influence our culture with respect to conservation and science through these roles; and primates perform these roles at zoos.

Meanwhile, we have come to an understanding of the complex manifestations of stress physiologically, behaviourally, and socially in primates (Honess & Marin, 2006). This complexity of suffering for zoo-primates means that from a utilitarian perspective, conservation benefits must outweigh big costs of suffering for zoos to be ethically defensible (Keulartz, 2015; Singer, 1973). Otherwise, the zoo-primates would suffer unnecessarily. In fact, accrediting bodies like the Association of Zoos and Aquariums (AZA) commit to matching welfare commitment with their conservation commitment (Hutchins et al., 2003). Without commitment to welfare standards that matches the commitment to conservation, a 'good accredited' zoo is no different to 'bad' road-side zoos (Hutchins et al., 2003). Whereas the value of the contribution of zoos to conservation is already being questioned by animal rights activists (Pierce & Bekoff, 2018; Safina, 2018), improving welfare is another aspect of the welfare utilitarian equation that zoos can control. Given how much control humans have on primate environments, agency in zoos and relationships with humans, we must therefore minimise any suffering that they experience while in our care (Hutchins et al., 2003; Keulartz, 2015; Safina, 2018). For zoo-primates who are constantly exposed to humans, we must understand how interactions or relationships between human and non-human primates affect their welfare.

Human-animal relationships in zoos are not as widely studied compared with animals on farms (Sherwen & Hemsworth, 2019). The reason for this difference is mainly economic. After World War II, humanistic motives of scientists involved in animal research diversified from medicine to industries that improve the economy (Kirk & Myelnikov, 2022). A majority of agricultural human-animal relationship studies focused on welfare and they were driven by the interest to drive up the productivity of their animals (Hemsworth & Coleman, 2011; Hosey & Melfi, 2014). Zoos share the desire for increased birth rates among their animals with the agricultural industry (Powell & Watters, 2017). However, increased productivity through improved welfare had major economic benefits for the agricultural industry, which meant that farm welfare research was funded by major businesses like McDonald's™ on top of funds from universities (Powell & Watters, 2017). Even though zoo welfare research started years ahead of farm welfare research, zoo welfare research was funded mostly through universities (Powell & Watters, 2017). Nonetheless, the understanding of human-animal relationships in zoos is emerging (Ward et al., 2018). However, the nature of interactions between humans and animals

in zoos is different to animals on farms where animals have been domesticated (Sherwen & Hemsworth, 2019). Hosey (2013) proposed that the key to understanding human-animal relationships in zoos is to understand the way animals perceive the benefits or threats that humans pose to them. The nature of human-animal relationships may be negative when animals perceive humans as a threat, neutral if animals view humans as conspecifics or inanimate parts of the environment, or positive if the animal benefits from the humans they encounter (Hosey, 2013). In zoos, humans play various roles: as keepers, veterinary health staff, or visitors. Each role has different potential consequences for the animals. It is therefore important to understand the nature of these different roles on zoo animal welfare. Meanwhile, zoos rely on visitor traffic to fund their operations and conservation projects. As a consequence, zoo primates are constantly exposed to visitors due to their role in conservation education. From a utilitarian perspective of animal welfare (Singer, 1973), zoos must ensure that animals do not suffer for the benefit of the educational services they offer. For my thesis, I focused specifically on the effect of visitors on the welfare of a species of zoo-housed primates, Sumatran orangutans (*Pongo abelii*).

Captive zoo-housed primates are well represented in studies of zoo visitor presence effects (Sherwen & Hemsworth, 2019). Historically, within the public and academic spheres, active critiques of primatological studies push for the inclusion of the welfare and rights of primates in scientific studies pertaining to human-animal relationships (Fuentes, 2012). Haraway (1989) even went so far as to accuse primatology of *simian orientalism,* which means that primatological studies were just concerned in finding origins of human behaviour without benefiting primates with their research. Singer (1993) started the *Great Ape Project* to recognise Hominids (chimpanzees, gorillas, and orangutans) as deserving of 'human' rights due to their similarities to humans (Bekoff, 1997). There is an inherent bias within the movement where animals with perceived cognitive capacities like humans are prioritised (Bekoff, 1997). While the *Great Ape Project* momentum did not necessarily reach many of the primates in captivity (Fuentes, 2012), the over-representation of captive primates in the zoo welfare literature (Fernandez et al., 2009; Sherwen & Hemsworth, 2019) reflects the same bias of the project. A majority of the welfare studies of visitor effects in zoos involved animals that were expected to react negatively and suffer cognitively (Sherwen & Hemsworth, 2019). Ironically, although primates have been studied extensively, the findings vary across species in terms of the valence of the effects, with rather vague implications for welfare (Sherwen & Hemsworth, 2019). There is a need for multiple indices which clearly measure specific constructs to be used to get clear interpretations of welfare implications (Sherwen &

Hemsworth, 2019). First, it is important to understand what welfare is in order to validate the choices of measures in these studies.

1.1 Animal welfare and visitor effect studies

The human understanding of welfare has changed throughout time (Broom, 2011). Animal welfare, as a measurable scientific concept, has its roots in the response of the scientific community to the public criticisms of animal handling on factory farms. After the publication of the book *Animal Machines* in 1964 (Harrison, 2013), the Brambell committee, a United Kingdom government committee led by the scientist Roger Brambell, was tasked to investigate the matter (Brambell, 1965). The Brambell committee reported the need for a biological understanding of the needs of each species. This was termed the *Five Freedoms*: Freedom from pain and disease, from hunger and thirst, from fear and distress, and to express normal behaviours (Brambell, 1965; Broom, 2011). Since then, the scientific community has faced difficulties in measuring animal welfare reliably and validly interpreting their measurements (For reviews see: Broom, 2013; Mason & Mendl, 1993). Scientists and veterinarians have had differing views about whether animal welfare should only include physiological health, affect and cognition, or both (Broom, 1986). The current most commonly held view is that welfare must include both the animal's physiological and psychological health (Broom, 1986, 2013; Dawkins, 2017; Mellor et al., 2020).

Broom (1986) defined welfare as the state of the animals' ability to cope physiologically and psychologically with their environment. Central to this definition of animal welfare is the idea that animals decide and/or behave in response to their environment (Broom, 1986, 2013; Dawkins, 1983, 1988, 2017). These responses by the animals fulfil certain needs; the inability to perform these needs would lead to frustration (Duncan & Wood-Gush, 1971). In other words, if animals fail to cope, their welfare is poor which would lead to suffering (Broom, 1986). The most recent conceptualisation of welfare called the *Five Domains of Welfare* maps the needs of animals onto the *Five Freedoms* mentioned above (Mellor et al., 2020). Mellor and colleagues (2020) argued that the cognitive domain needs of the animals arise from the fulfilment of health, environmental, and nutritional domain needs of the animals mediated by responses in the behavioural domain. Regardless of the terminology used, it is evident that the core element of the animals' ability to cope with their own needs (across the five domains) and the environment is still central to how welfare should be measured. Welfare measures should answer two questions succinctly summarised by Dawkins (2017): "Is the animal healthy? Did the animal get what it wanted?" (p.4)

In terms of visitor effects on captive animal welfare, research demonstrates mixed negative, positive or neutral effects depending on the species that participated in the research (For a review see: Sherwen & Hemsworth, 2019). However, Sherwen and Hemsworth (2019) found that a majority of published studies reported "negative effects". Those studies that found negative effects measured either behavioural changes or glucocorticoid level changes or both (e.g., in orangutans: Birke, 2002; in western lowland gorillas: Clark et al., 2012; in cotton top tamarins: Glatston et al., 1984; in Mexican wolves: Pifarré et al., 2012; in gibbons and siamangs: Smith & Kuhar, 2010; in chimpanzees: Wood, 1998). Changes in behaviours like foraging have been used as indices of negative effects (Sherwen & Hemsworth, 2019). However, the welfare consequences of these changes in behaviours may be difficult to interpret (Sherwen & Hemsworth, 2019). Sherwen and Hemsworth (2019) argued that changes in foraging are still important to note as restriction in foraging due to visitors may result in diminished welfare. It is also important to note that most of these studies focused on visitor presence across the day, which means that the data could have been confounded with other variables that were simply correlated with visitor numbers, such as keeper routine, weather, feeding schedules, and animal shifting schedules. As evidence for this, Goodenough et al. (2019) studied ring-tailed lemurs (*Lemur catta*) and found that when these variables were kept constant, visitor numbers did not explain the purported negative effects (Goodenough et al., 2019). This raises the question: have these studies truly measured the effects of visitors on welfare?

Some studies that reported negative visitor effects on welfare measured changes in the behavioural and physiological "stress response" of the species (Sherwen & Hemsworth, 2019). Prolonged exposure to stress has pathological consequences not only for the mind but also for the physiology of animals (McPhee & Carlstead, 2010). This is because the endocrine pathways that respond to stress also modulate other bodily functions, such as immune response, digestion, and reproduction (Dhabhar, 2014; McEwen, 2008; Mönnikeset al., 2001; Romero et al., 2009). Chronic stress overtaxes these systems resulting in 'physiological wear and tear' (Romero et al., 2009). Prolonged stress therefore disrupts the balance of organ system which results in problems in their functions. For example, while short term stress enhances the immune functions to enable faster healing, a chronically overactive immune system due to chronic stress can cause autoimmune diseases (e.g., lupus, psoriasis) (Dhabhar, 2014). Chronic psychosocial stresses when combined with metabolic stress (exercise) has also been shown to disrupt the reproductive cycle and induce amenorrhea in crab-eating macaques (Williams et al., 2007). In mammals, prolonged cortisol elevation is linked to reduced bone density, similar

to bones seen in humans with Cushings syndrome (for review see: Suarez-Bregua et al., 2018). In a series of gruesome experiments, Brady (1958) demonstrated how repeated electric shocks resulted in duodenal ulcers followed by death in macaques. In these experiments, only the macaques who were able to press a lever to 'control' the shocks acquired ulcers; suggesting that stress was the cause of the ulcer (Brady,1958). In rats (*Rattus norvegicus*), fear of novelty predicted the magnitude of the corticosterone response and even early death (Cavigelli & McClintock, 2003). Thus, prolonged stress has implications for the suffering of the animals within the *Five Domains* of welfare; hence, stress has welfare consequences. In other words, stress is a sign of a failure to cope – a sign of poor welfare. Therefore, it is important to understand visitor effects of animal welfare through the lens of coping and stress.

However, the concept of stress is often conflated with the arousal response which is not specific to certain stimuli (Broom, 2011). Cortisol, a hormone used to capture the physiological arousal response, also plays a role in the mobilisation of energy (Cavigelli, 1999). In humans, behaviours like exercise, or even activities that elicit positive emotions may result in an increase in cortisol levels (Cavigelli, 1999). To disambiguate the concept of stress, Kim and Diamond (2002), presented a model of stress that integrates the relationship between behaviour, cognition, and hormones. In their model, corticosteroids measure the arousal caused by a certain stimulus. Whether an event is stressful or not depends on the individual's perception of the aversiveness of the stimulus and control over the situation. While animals cannot verbally report their perception of aversiveness and control, they can modify their behaviour to control or cope with their environment (Dawkins, 2017). Therefore, in order to capture the relationship between visitor presence and the stress response of zoo-housed animals, one must analyse aversive behaviours and indicators of arousal. This multi-dimensional interpretation of stress and welfare is missing in the literature on visitor effects in captivity due to reliance on single measures (Sherwen & Hemsworth, 2019).

Starting in March 2020, the COVID-19 pandemic resulted in widespread lockdown measures that prevented visitors from visiting zoos. Fortunately, these lockdowns came with the opportunity to study the effects of the presence and absence of visitors across weeks and even months during the lockdown and when visitors were reintroduced. This means that visitor numbers varied independently of the time of the day. This opportunity, therefore, allows research to further improve measurements of welfare regarding visitor effects while simultaneously addressing the confounding variables that used to be common in visitor effect studies. During the era of COVID-19 lockdowns, visitor effect studies have started to use multiple indicators of stress. Among the most used indices of stress, enclosure space use and

fecal cortisol were used to indicate aversive behaviours and arousal/stress respectively (e.g. Edes et al., 2022, Williams et al., 2022). Other behaviours like activity levels were still used to add context to the indicators of stress (Edes et al., 2022, Williams et al., 2022). Of the visitor effect studies conducted during the COVID-19 lockdowns, the majority of studies reported little to no behavioural or physiological changes when visitors were reintroduced (e.g., Bernstein-Kurtycz et al., 2021; Edes et al., 2022; Finch et al., 2022; Frost et al., 2022; Kidd et al., 2022; Masman et al., 2022; Powell & Edes, 2023; Salak & Barbour, 2022; Williams et al., 2022). For example, among Western lowland gorillas (*Gorilla gorilla gorilla*) and bonobos (*Pan paniscus*) at the Twycross Zoo in the UK, the primates were more active when visitors were introduced than during the lockdown (Williams et al., 2022). The gorillas, bonobos, and chimpanzees (*Pan troglodytes*) in that study did not show changes in exhibit space use or cortisol levels (Williams et al., 2022). The same findings were found in gorillas, banteng (*Bos javanicus*), polar bears (*Ursus maritimus*), and grizzly bears (*Ursus arctos*) (Edes et al., 2022). These studies, which measured both aversive behaviours and arousal, suggest that the animals were not stressed by visitor presence. By contrast, Krebbs and colleagues (2023) studied zoo animals that were exposed the most to visitors such as reticulated giraffes (*Giraffa reticulata*), Chilean flamingos (*Phoenicopterus chilensis*), meerkats (*Suricata suricatta*), and prairie dogs (*Cynomis socialis*). They found that all their study species showed changes in behavioural indicators of arousal at both very low and very high visitor counts. They suggested that these results support the idea that moderate visitor counts signal that predators are not present; they called this the "dither effect". This dither effect model was intended to replace the original model of visitor effects by Hosey which sees visitor effects as positive, negative or neutral. However, the Krebbs et al. (2023) study did not take advantage of the lockdown to remove the confounding variables that vary with visitor numbers across the day. Instead, they divided the day into hours and used the lockdown to simply get data from times where there were fewer visitors. They also included zookeepers in their visitor counts, which may be another confounding variable.

1.2 Sumatran orangutans and visitor effects on their welfare

The purpose of this study was to assess the visitor effects on the welfare of Sumatran orangutans when COVID-19 lockdown measures were lifted at the Toronto Zoo. The Sumatran orangutan is a species of orangutan found in Sumatra, Indonesia (Delgado Jr & van Schaick, 2000). They, along with the Tapanuli and Bornean orangutans, belong to the same family (Hominidae) as humans, chimpanzees, bonobos, and gorillas. Given their hominid status, the effort to improve the wellbeing of Sumatran orangutans in captivity is understandable because

of the assumption and evidence (Russon, 1998; 2002) that they are cognitively complex. Their cognitive complexity motivates some people's concerns for improving welfare. Whether the notion that cognitive complex animals like great apes should be at the forefront of welfare studies is ethical or not is beyond the scope of my thesis (but see Bekoff, 1997 for arguments). Welfare based decisions focus on how much the animal thrives or suffers because of the changes we or the environment imposes on them. Cognition is just one aspect of animal welfare. However, Sumatran orangutans are also critically endangered and are projected to decrease to only 4,500 individuals left in the wild by 2030 (Wich et al., 2016), meaning that there may at some point be more orangutans living in captive settings than in the wild. It is pragmatic and also ethically and morally justifiable (Hutchins et al., 2003; Singer, 1973) to ensure that the captive setting is conducive to their wellbeing. Furthermore, their status as close cousins to humans means that our species benefits from comparative research (MacDonald & Ritvo, 2016) and education of zoo visitors (Carr, 2016; Patrick & Caplow, 2018; Whitworth, 2012). Measuring and understanding the effects of visitors on Sumatran orangutan welfare will help ensure that their lives in captivity are not compromised by suffering.

As modelled by Hosey (2013), the nature of interactions between visitors and animals varies with respect to whether the animals perceive visitors as threats, resources, or simply neutral. In the case of free ranging Sumatran orangutans, humans do pose threats in terms of encroachment of resources and fatal confrontations. In contrast to the other great apes, orangutans in general are semi-solitary and primarily arboreal (Delgado Jr & van Schaick, 2000). This semi-solitary fusion-fission social organisation is due primarily to the uneven and unpredictable availability of food in Southeast Asian rainforests (Delgado Jr & van Schaick, 2000; Russon, 2010). Orangutans primarily forage alone unless the orangutan is a female with an offspring or a consort, or they are sharing trees that bear large quantities of fruit during masting years (Delgado Jr & van Schaick, 2000; Russon, 2010). However, this does not mean that orangutans live isolated from others. Orangutans have cultural variations in foraging behaviour across specific geographic locations that they acquire through observing nearby conspecifics (Russon, 2002). Nonetheless, the sensitivity of their social structure to resource availability makes orangutans susceptible to human encroachment. Additionally, human hostility towards wild orangutans has existed throughout history and until the present time. There is anthropological evidence of humans hunting orangutans' pongid ancestors (Delgado Jr & van Schaick, 2000). Currently, wild orangutans face the threats of hunting for bushmeat, habitat destruction due to logging and aggravated climate change, retribution killing for crop raiding, and poaching for the pet trade (Campbell-Smith et al., 2012; Drake, 2015; Marshall et

al., 2006; Meijaard et al., 2011; Nijman, 2017). Humans have created an environment for wild orangutans that is rife with violence and destruction. It is therefore unsurprising that wild orangutans show an increase in fecal cortisol when exposed to tourists (Muehlenbein et al., 2012). Whether the same is the case for Sumatran orangutans in captivity is unclear as visitors usually do not compete for food nor inflict violence towards orangutans in this context.

Meanwhile, visitor effect studies on captive orangutans offer ambiguous evidence with respect to measuring and interpreting welfare consequences. Most studies used ambiguous measures, like looking behaviour, infant holding behaviour, or head covering behaviour, with the aim of quantifying fear or simply behavioural change (Sherwen & Hemsworth, 2020). While multiple behaviours were initially sampled, post-hoc interpretations of changes heavily relied on single behaviours (Sherwen & Hemsworth, 2020). It is important to note that these behaviours on their own do not directly indicate the valence (i.e., pleasant vs unpleasant) of visitors nor the state of arousal the animal was in due to visitors. For example, Birke (2002) asked visitors to make noise and found that orangutans increased the rate of looking at visitors compared to when visitors were quiet (Birke 2002). Birke (2002) suggested that direct gaze for orangutans is aggressive which led them to interpret their findings as a sign that the orangutans were disturbed by visitor noise. On the other hand, Bloomfield and colleagues (2015), found that orangutans approached open windows where visitors were visible and present. They suggested that these findings implied that the orangutans did not find the visitors aversive, and that there was positive welfare associated with visitors. A study on the captive Sumatran orangutans of the Singapore Zoo found that orangutans increased their begging behaviours when visitors were engaged than if visitors were passive (Choo at al., 2011). To my knowledge, only one study combined multiple indices of stress in measuring visitor effects on orangutan welfare. In the closely related Bornean orangutan (*Pongo pygmaeus*), Amrein and colleagues (2014) found that cortisol levels of younger orangutans increased with an increase in number of guests while older orangutans increased their rates of self-directed behaviour. Both self-directed behaviours and cortisol increase were taken as signs of stress. However, as discussed above, there is ambiguity to the stress response such that the 'signs of stress' indicate both positive (i.e., excitement) or negative arousal (i.e., stress) depending on whether or not an individual finds the change aversive. Because stress indicates the animals' failure to cope with the changes in their environment, it is necessary to evaluate their stress response to understand the effects of environmental changes on their welfare. Therefore, to understand the welfare consequences, one must ask: Did the orangutans show signs of aversion towards the visitors? Did they show behavioural signs of arousal? Did they show physiological signs of arousal?

Alternatively, were there other factors that affected the behavioural changes that were associated with visitor presence?

1.3 Hypothesis

I used the same questions in assessing the welfare effects of visitor reintroduction for my thesis. I first defined welfare as the state of an animal's capacity to cope with aspects of or changes in their environment. I further defined the animal's capacity to cope using physiological and behavioural measures of stress to understand how the animal responded to changes in the environment. The reintroduction of visitors after a prolonged period of absence during the COVID-19 lockdown presented an opportunity to study coping through a natural experiment. *I hypothesised that if the welfare of the orangutans was affected by visitor reintroduction, then there would be changes in their aversive behaviours as well as in their behavioural and physiological indicators of arousal*. *If there were more aversive behaviours and greater arousal during visitor reintroduction than lockdown, then the orangutans were stressed by the visitors.* Additionally, *if other factors (e.g., conspecifics, keeping staff) explained the behaviours and location of the orangutans, then there should be strong associations with these factors and the behaviours of the orangutans.* I further explain the specific predictions I made in the following sections.

1.3.1 Aversive behaviours

If the orangutans changed their aversive behaviours towards the visitors, then *the orangutans should reduce their use of physical space, exhibiting a specific preference for the areas closest to the off-exhibit space during visitor reintroduction compared with the lockdown phase*. Additionally, *the orangutans should increase the amount of time they spent hiding*. These two changes indicate avoidance of visitors or a preference for something other than being close to the visitors.

1.3.2 Behavioural and physiological indicators of arousal

If the orangutans increased their arousal during visitor reintroduction then the amount of time they spent foraging should decrease and the amount of time they spent inactive should change. Physiological arousal disrupts digestion and sleeping (i.e., rest and digest) to promote the "fight or flight" response. In animal models, feeding behaviour either decreases or increases in response to physiological arousal due to downstream effects of the hormones cortisol and corticotrophin releasing hormone (CRH) on hormones that stimulate hunger (e.g., leptin and ghrelin) (For a review: Maniam and Morris, 2012; in rats: Percoraro et al., 2012; Martí et al., 1994). Similarly, stress has also been shown to disrupt sleeping patterns (Boccia, 1995). If the orangutans responded with physiological arousal to visitor reintroduction, they would spend

less time foraging when compared to the lockdown phase. This is because in the visitor introduction phase they would either finish their food faster or would refuse to forage for more food when compared to the lockdown phase. While I did not directly test sleeping patterns, I expected that inactive behaviours would also change when visitors were introduced if the orangutans responded with arousal. Similarly*, displacement behaviours towards the self, conspecifics, and objects as well as agitated movements should increase* during visitor reintroduction when compared with the lockdown. These behaviours have been traditionally used to indicate arousal and anxiety in primates (Caine, 2017; Murakami et al., 2017; Troisi, 2002). Displacement behaviours, like self-directed behaviour, agonistic behaviour, and object directed displacement, and agitated movements have been found in studies to decrease after administration of anxiolytics suggesting their relationship with the arousal response (Schino et al., 1991).

Furthermore, to ensure that the measures were sensitive enough, I included fecal consistency as a physiological measure of arousal. *If the orangutans were negatively aroused by the reintroduction of visitors, there should be an increase the number of stool samples with abnormal consistency*. The biggest predictor of abnormal fecal consistency in humans is chronic stress and diet (Lemay et al., 2021; Welgan et al., 1995). Thus, we could expect the same for orangutans whose digestive systems are essentially identical to humans (Chivers & Hladik, 1980).

1.3.3 Effects of keeper and conspecifics

If the orangutans' behaviours were influenced by their keepers, then *the orangutans should increase their keeper directed behaviours the greater the frequency of visits of the keepers*. If the orangutans were generally searching for *the keepers, then there should be an inverse relationship between the scanning behaviours of the orangutans and the frequency of the keeper visits*. Further, it would be important to note whether the paired orangutans were using the same areas of the exhibit.

2. Methods

2.1 Subjects

All six zoo-housed Sumatran orangutans (2.4) of the Toronto Zoo participated in this study. Table 1 describes the orangutans in detail along with whom they were housed with, and the number of hours they were observed across the phases of the study (Lockdown vs Visitor reintroduction). Each orangutan had a different housing condition (paired or single) either with a relative as with Jingga and Ramai or as a social/breeding pair like Sekali and Budi. Ramai was also occasionally paired with Budi on and off-exhibit as a temporary breeding pair. With the exception of Puppe, all orangutans were zoo-born; thus, have always been exposed to visitors when they were on exhibit.

Table 1

The Sumatran orangutans (Pongo abelii) of the Toronto Zoo

Individual	Age	Sex	Paired/Solitary	Hours Observed (Lockdown)	Hours Observed (Visitor)
Jingga	15	Female	Paired(Ramai)	41.5	32.83
Ramai	36	Female	Paired(Jingga)	41.17	39.17
Budi	15	Male	Paired(Sekali)	52.5	46
Kembali	15	Male	Solitary	20.5	8
Sekali	28	Female	Paired(Budi)	54.5	43.83
Puppe	54	Female	Solitary	58	39.40

The orangutans were given free choice between going on exhibit or staying in their off-exhibit space (from herein: holding). Once on exhibit, the orangutans were kept in for half the day or a full day. Therefore, the orangutans were not observed for an equal number of hours. This was particularly the case with Kembali, who was not observed as much as the other orangutans. Kembali refused to stay on exhibit. The reason for this was not apparent. However, throughout the study, breeding regularly occurred in the holding between the flanged male Budi

and Sekali or Ramai. The keeping staff suggested that this was one of the reasons why he chose to stay in the holding.

2.2 Sampling protocol

I sampled behaviours using point-scan sampling with 10-minute intervals to understand the amount of time taken by each behaviour. I also used *ad libitum* sampling for behaviours that were rarely observed and typically short in duration (i.e. < 1 minute per bout), particularly, Agitated movement, Agonistic behaviour, object directed displacement, and self-directed behaviours occurred. Table 2 shows an ethogram of the Sumatran orangutans in this study. Observation sessions happened approximately two hours in the morning (0830 h–1230 h) and two hours in the afternoon (1240h–1600h). The observation sessions began on 3 May 2021 and ended on 17 August 2021. Originally, the study had three phases (Lockdown, Limited visitors, and fully opened). However, because of the short amount of time with limited visitors (5 July–16 July), there was not enough time to gain enough sample hours for all the orangutans. After comparing the data from the two visitor phases to show that they were not significantly different from each other, I combined the limited visitor phase with the fully opened phase.

Table 2

Ethogram of behaviours for Pongo abelii

Category	Code	Description
Foraging	F	Consumption of plant matter (e.g., leaves; soft vine barks; soft stalks, round fleshy parts). Marked by insertion of plant matter into the mouth with the use of the hands. It starts with the use of the hands to pick plant matter from a bunch or pile, to pick apart plant matter and to break plant matter into small pieces. The hands are then used to bring plant matter into the mouth. This is followed by chewing (i.e., open and close movement of the jaw while the plant matter is either partially or fully in the mouth). This is culminated by swallowing; that is, the plant matter is no longer in the mouth nor outside the animal and the animal moves to get more. The bout stops when there is a pause in the behaviour > 3 s or another behaviour is performed.

Locomotion	L	The orangutan moves with the use of limbs from one point in the exhibit to the next point at least within a metre away from the origin. The orangutan may end up in the same location as the origin, but along the path should have gone at least a metre away from the origin. The orangutan may be locomoting bipedally or quadrupedally on plane surfaces like platforms and the ground. If the orangutan is on climbing structures but is supported by all 4 limbs, the movement is classified as locomotion.
Object Play	OP	Repetitive manipulation and inspection (visual and/or tactile) of inedible objects which are not part of another individual's body. The individual is visibly engaged (i.e., the facial/head orientation is on the object being manipulated). Inspection or manipulation is done by mouth, hands, or feet). Movement may appear like other behavioural categories but the size/ speed of movements of limbs are exaggerated.
Fiddling	FD	Slow and repetitive manipulation of an object with *no apparent purpose or engagement* (i.e., the orangutan may appear like staring in space and the gaze is not directed towards the moving object). Manipulation may be subtle repetitive finger movements along the object being manipulated
Inactive	I	The animal stays in the same spot or turns around but does not go beyond a metre from origin. The animal is not engaged in self-directed behaviours, defecation, urination, foraging, hiding, defecation or urination or scanning behaviours or social interaction. The animal may be lying prone, supine, sideways, upright sitting, or quadrupedal but stationary.
Affiliative	AF	The animal engages in social interactions with another individual such as allogrooming, begging for food, food sharing, hugging, tolerance. Behaviours would appear to maintain bond as seen by maintenance of close proximity. These

		behaviours do not have audible vocalisations or vigorous movements.
Agonistic	AG	Social interactions with individuals where distance from each other is the outcome unless there is a physical confrontation or fight. The animal may be engaged in, rejection of begging, or avoidance, or vigorously grabbing food from the grasp of the receiver of the interaction. Characterised by vigorous movements towards or away from the other individual.
Keeper directed	KD	Staring, following, locomoting towards the keeper, or obtaining food from the keeper. Attention/ head orientation must be placed on the keeper. The keeper should be visible around the perimeter of the exhibit or in the keeper's cage.
Guest-directed	GD	Staring, following, or moving towards the guests. Attention must be placed on the guest. Volunteers (humans in white shirts and beige trousers) are considered guests.
Self-Directed	GR	Inspection of hair, body or mouth with hands, feet, mouth or with the use of objects such as browse, sticks or enrichment. The body part being inspected is prod repeatedly by any of the abovementioned implements. The animal may scratch, squeeze, poke or pinch the body part being inspected. Attention/gaze does not have to be on the body part.
Hiding	H	The animal covers itself with a blanket, a leaf, or goes in the bucket such that only a portion of the head is visible for scanning.
Urinate	U	Marked by the presence of darker wet spot on the floor. Urine flows from the hind of the orangutan. The orangutan may be hanging on climbing structures using any combination of limbs or may be sitting at the edge of the moat, platform, or on a bar with the hind facing where the urine would land.

Object Manipulation	OM	Moving objects with limbs or the mouth from one point in the enclosure to the other point. There is a very clear purpose that usually stops once the purpose has been achieved.
Scanning	SC	The animal makes a short sweeping movement of the head, and the eyes stay forward following the gaze. The attention must be on anything outside the exhibit. The animal may be sitting on the floor or bipedally/ quadrupedally locomoting towards a window or the edge of the exhibit.
Patrolling	PT	The animal follows a repeated path around a portion or the entirety of the perimeter of the exhibit. The animal seems vigilant with repeated scans as movement happens.
Defecate	D	Marked by the presence of fecal matter on the floor. Faeces drops from the hind of the orangutan. The orangutan may be hanging on climbing structures using any combination of limbs or may be sitting at the edge of the moat, platform, or on a bar with the hind facing where the faeces would land. The orangutan may also reach around such that the faeces would land on the palm and the orangutan would drop the collected faeces on the floor. The orangutan may also gradually orient the upper body from an upright sitting position to a more acute prone posture.
Agitated movement	AM	Locomotion that is fast, with fast scanning of surroundings, may or may not stop at a destination. Usually follows a loud noise. Brachiation along the bars is hasty and may involve short airtime. Scans towards the keeper's kitchen or the entrance to the exhibit may be possible.
Object Directed Displacement	AB	Objects are touched with the use of the hand or other body parts. The contact may be brief or prolonged. Includes head slamming onto blankets where recoil happens after contact. May also be forceful fabric tearing wherein the orangutan uses both hands to pull fabric apart in opposite directions swiftly and with recoil.

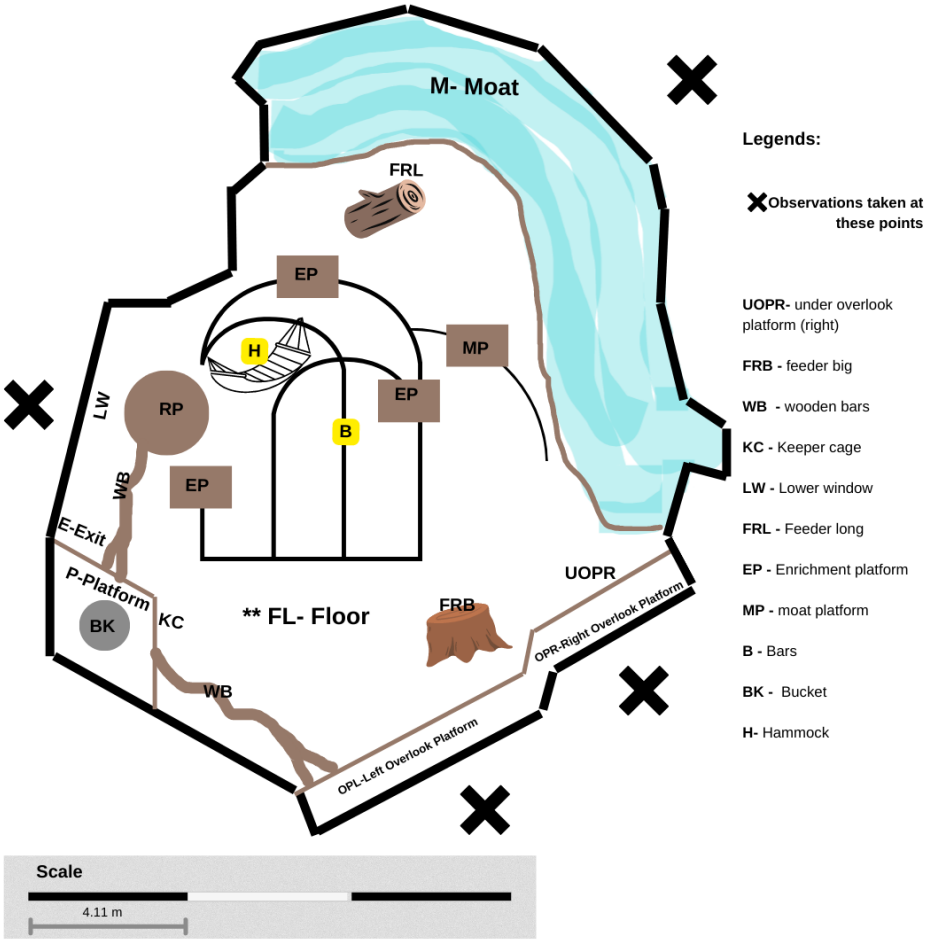


Figure 1. Toronto Zoo Sumatran Orangutan Indoor Exhibit Schematic Diagram. The biologically relevant areas are labelled with their codes. FL - The whole floor except other defined areas**.**

Figure 1 shows a schematic diagram of the orangutan enclosure, the biologically relevant areas within the exhibit, and the public area where I took the observations. I noted the enclosure areas where orangutans were at each time-point at the same time as the point scans.

The keeping staff collected the fecal samples each day before 1000 h for all orangutans whether they were on exhibit or not. The samples were placed in resealable bags and frozen until ready to be evaluated. Within an hour of thawing the samples for extraction, I rated the fecal consistency of the samples using the Bristol stool scale (Table 3) . The fecal sample collection and behavioural sampling collection did not start at the same time. I've restricted the fecal samples between 8 June 2021–3 August 2021. Because it was possible to collect fecal

samples from all the orangutans each day, I gathered a total of $N = 210$ fecal samples even with a shorter sampling period.

Table 2

Bristol Stool Form Scale

Type	Description
Type 1	Separate hard lumps, like nuts
Type 2	Sausage-shaped but lumpy.
Type 3	Like a sausage or snake but with cracks on its surface
Type 4	Like a sausage or snake, smooth and soft
Type 5	Soft blobs with clear-cut edges.
Type 6	Fluffy pieces with ragged edges, a mushy stool.
Type 7	Watery, no solid pieces.

Note. From "Stool Form Scale as a Useful Guide to Intestinal Transit Time," by S.J. Lewis & K.W. Heaton, 1997, *Scandinavian Journal of Gastroenterology*, *32*(9), p.920-924 (https://doi.org/10.3109/00365529709011203). Copyright 1997 by Taylor & Francis.

2.3 Statistical analyses

I compared the measures between the lockdown phase (3 May 2021–4 July 2021), where there were zero visitors allowed in the pavilion, and the visitor phase (5 July 2021–30 August 2021) where a maximum of 200 people were allowed in the pavilion. The alpha level for all analyses was $\alpha = 0.05$. To assess the effect sizes, I reported the 95% confidence interval for the parameter estimate of concern. I conducted all statistical analyses using R (R Core team, 2020). I describe the particulars of the analyses in the following sections.

2.3.1 Behavioural samples

I summarised behavioural data that were sampled with the scan sampling method as relative frequencies (i.e., percent of scans). Additionally, I summarised the behaviours that were sampled using *ad libitum* sampling as rates per minute. I summarised the relative frequencies and rates between the phases for each individual and for each observation session.

I considered each observation session for each observed individual as the statistical unit in the following analyses. I modelled the relationship between the behavioural indicators and phases of the study using the 'lme4' package (Bates et al., 2015) to implement linear mixed effects models. This procedure is an equivalent of the repeated measures Analysis of Variance (ANOVA) without the restrictive sphericity assumption. I used rate or relative frequency as the response variable, phase as the predictor variable and individual as the random variable.

2.3.2 Enclosure use

I first measured the volume (m^3) of each exhibit area and summed all the volumes of each area to yield the total usable enclosure volume. I then transformed the volumes of the biological relevant areas to the percentage of total usable enclosure volumes. I measured the selectivity of enclosure areas using the modified spread of participation index (SPI) (Brereton & Fernandez, 2021; Ross et al., 2011). This considers the estimated percent of total enclosure volume for each area into the calculation of the expected frequency of use. I used the sum of the frequencies of scans an orangutan was seen in each area as the observed frequency. The modified SPI equation yields a score between 0–1 (0 being equal use and 1 being unequal use). Each orangutan had an SPI score for each phase. These SPI scores were the statistical units for this analysis. I compared the mean SPI score across each phase using a linear mixed effect model with the SPI as the response variable, phase as the predictor variable and individual as the random variable. I made note of the most used location for each phase to understand what location was preferred the most.

2.3.3 Fecal consistency

I categorised the fecal consistency scores <3 and >4 as abnormal (scored as 0 for normal or 1 for abnormal) per the original classification suggested by Lewis and Heaton (1997). These scores are indicative of diarrhea or constipation in human fecal samples. I estimated the log-odds of abnormal fecal samples using a generalised linear mixed effect model with a log-link function using the 'lme4' package. I modelled the log-odds of abnormal fecal consistency with the phase (lockdown vs visitor) as a response variable and the individual as the random variable. I also added presence on exhibit (on exhibit or off exhibit) as another predictor variable to control for whether the orangutan was on exhibit or not. I did not use an interaction model because it would imply that only days when the orangutans were on exhibit produced abnormal faeces. However, I was interested in chronic stress which was what fecal consistency reflected (Lemay et al., 2021). This meant that non-exhibit days could also yield abnormal fecal samples, especially because the intestinal transit time for orangutans varies (range in humans: 10–73 hours, Lee et al., 2014). I used maximum likelihood estimation (reported as Z-scores)

to assess the significance of the effect estimates (reported as odds-ratios). I used the Chi-square statistic to assess whether the model predicted the variability in the log-odds of abnormal fecal consistency better than a model only predicted by individual differences.

2.3.4 Effects of conspecifics and keepers

To understand the effects of the keepers on the behaviour of the orangutans, I used linear mixed effects models on the rates of keeper directed behaviours and scanning behaviours predicted by the rate of keeper presence with individual as the random variable. Additionally, I reported the percent of scan samples the paired orangutans were observed using the same areas of the exhibit.

2.4 Ethics statement

All observations were done in the public areas of the zoos. The zero-visitor phase was implemented by the Toronto Zoo as part of their pandemic control strategy. I merely observed the orangutans across the Zoo's implementation of the process. Therefore, this study did not cause any additional risk to the Orangutans outside of what they already face in their daily lives.

3. Results

3.1 Aversive Behaviours

I analysed the physical space used by the orangutans to understand whether or not they were avoiding the visitors. This would indicate whether or not the orangutans saw the visitors as aversive. For example, if the orangutans avoided human presence, I would expect to see more unequal space use with stronger preference toward areas away from visitors, compared to their space use during the lockdown. In other words, I should see higher spread of participation indices (SPI) during the visitor reintroduction compared to the SPIs during the lockdown. As seen in Figure 2, the reintroduction of visitors after the lockdown measures did not significantly affect the amount of space in the habitat that the orangutans used (t (5) = –0.96, p = .38). The orangutans did not modify their exhibit use in response to the reintroduction of visitors in their pavilion and did not avoid areas close to visitors when visitors were reintroduced. Based on this information alone, for the orangutans, the visitor reintroduction phase was not any more aversive than the lockdown.

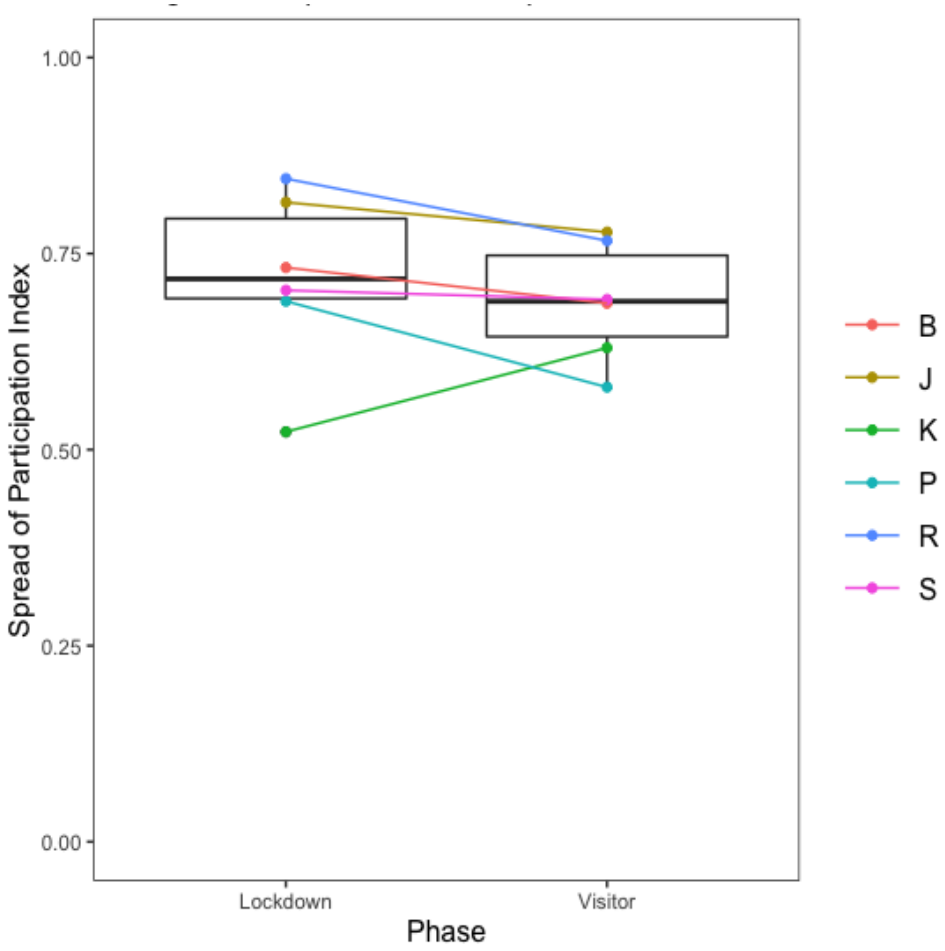


Figure 2. The enclosure area selectivity of the Toronto Zoo orangutans across the phases of this study (Lockdown vs Visitor Phase). The initials represent each orangutan (B = Budi, J = Jingga, K = Kembali, P = Puppe, R = Ramai, S = Sekali).

However, it is important to note that the orangutans were already very selective in what areas of their habitat they used. The orangutans spent a majority of the time (38 % during the lockdown, 25% during the visitor phase) at the back platform (Figure 1). This area is close to where the keepers enter the exhibit area to provide more food and enrichment, as well as close to the exit to the orangutan holding (off exhibit space). Because their SPI scores were close to 1, this suggest that the orangutans strongly preferred spending time at this location rather than other locations in the exhibit. These orangutans are captive born and thus, not naïve to visitors. It is possible that the orangutans may have sat in this area to avoid visitor interaction and in order to minimize the distance from the exit. However, this seems unlikely because the orangutans did not increase hiding behaviours when visitors were reintroduced (Figure 3) suggesting that they did not find visitor presence aversive. In fact, when compared to the lockdown, the orangutans decreased their hiding significantly (t (245.53) = –3.61, p = .0004) when visitors were introduced.

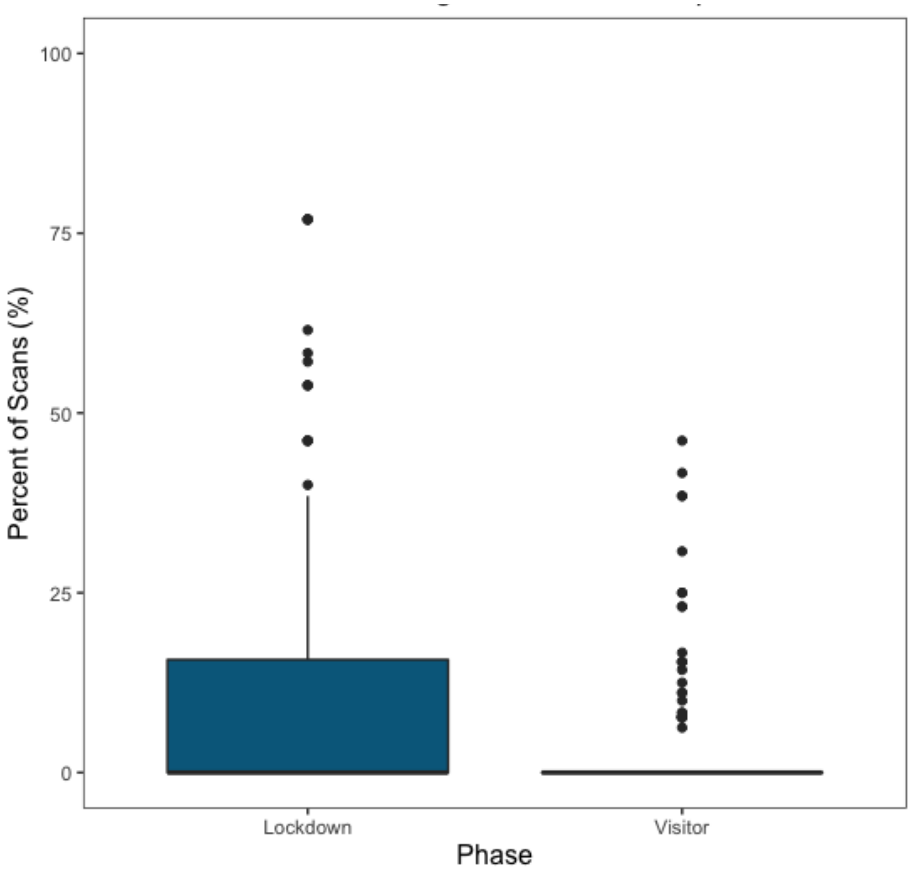


Figure 3. The percent of scans the orangutans were observed hiding across the phases of this study (Lockdown vs Visitor).

It is possible that the orangutans may prefer this area for other reasons such as proximity to keepers in anticipation of enrichment and provisions, which I will discuss in a later section. Despite the evidence pointing towards the lack of aversiveness of visitor introduction, it is

valuable to understand how effective the behavioural response of the orangutans was to mitigate possible stress from the visitors. Whatever the reason is for choosing the back platform, it could potentially limit the capacity of the orangutans to cope through hiding or avoidance when visitors were introduced. For example, to be close to the keeper entrance, the orangutans could have chosen to stay visible despite finding the visitors aversive. If this was the case, I would expect the orangutans to be in a state of higher arousal during visitor introduction. Looking at behaviours that are indicators of arousal states of the orangutans would help clarify this.

3.2 Indicators of arousal

3.2.1 Foraging and inactivity

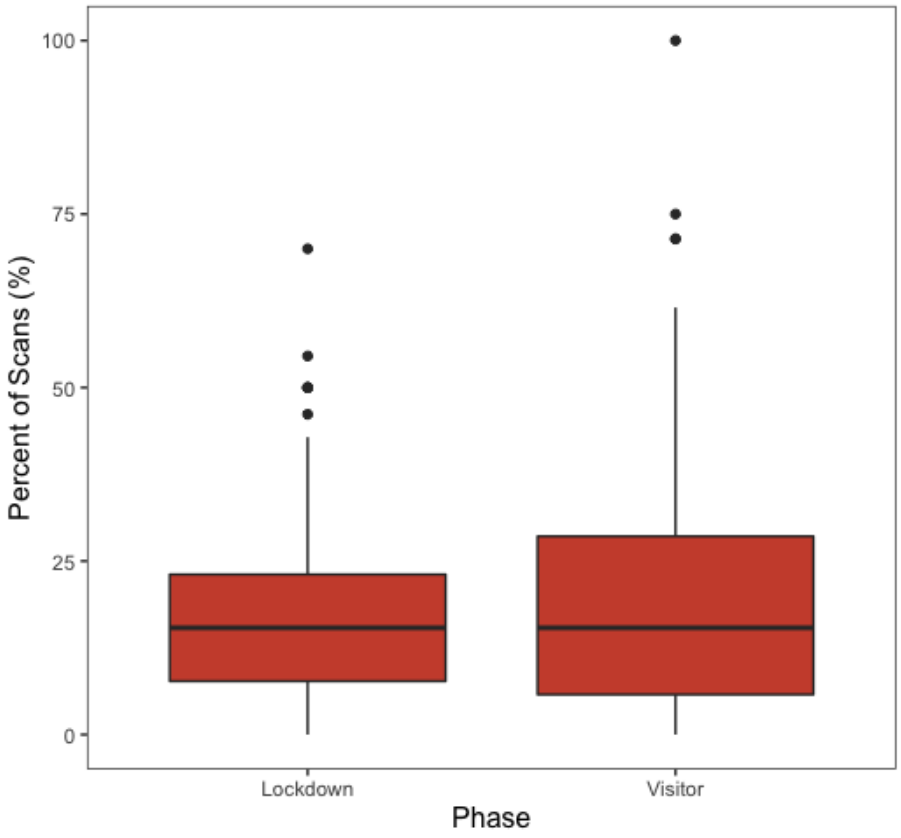


Figure 4. The percent of scans the orangutans were observed foraging across the phases of this study (Lockdown vs Visitor).

Because the arousal response disrupts the pathway that promotes eating and sleeping (i.e., "rest and digest" behaviours), the orangutans should decrease the amount of time they spent foraging and change the amount of time they spent sleeping if their arousal levels increased during visitor reintroduction. The orangutans, however, did not change the frequency of their "rest and digest" behaviours between lockdown and visitor reintroduction. As shown in Figure 4, there was no difference (t (246.25) = 1.503, p = .13) between the mean percent of scans the orangutans spent foraging during the lockdown phase Similarly, there was no

difference (t (245.02) = 1.60, p = .11) between the mean percent of scans the orangutans spent inactive during the lockdown and the visitor phase (Figure 5). This suggests that "rest and digest" behaviours (i.e., behaviours that remain consistent when the animals are not in "flight or fight" mode) were not affected by the reintroduction of visitors into the exhibit. Thus, the lack of changes in these behaviours when visitors were introduced suggests that the duration and intensity of the arousal was not enough to disrupt non-flight or fight functioning. Nonetheless, the arousal could have been transient enough that time was not necessarily taken away from performing the "rest and digest" behaviours. Thus, it is important to also analyse the change of displacement behaviours (i.e., behaviours directed towards the self, others, or objects), agitated movements, and physiological response – all of which are considered hallmarks of high arousal in primates (Caine, 2017; Murakami et al., 2017; Troisi, 2002; Welgan et al., 1995).

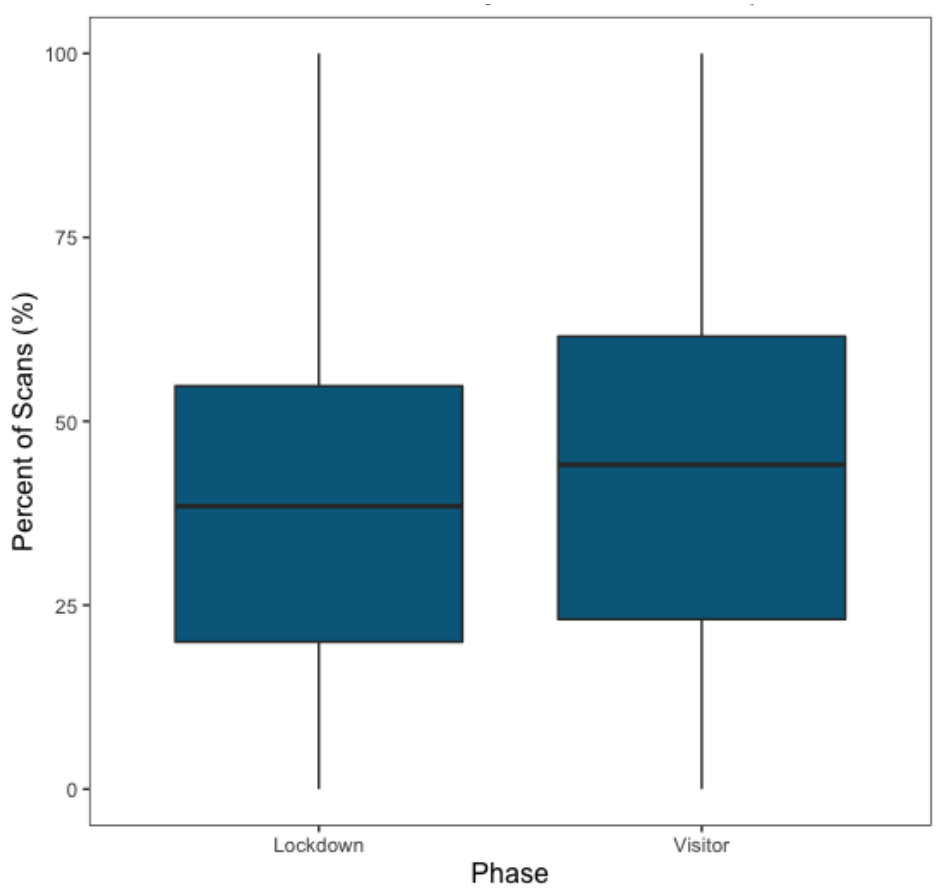


Figure 5. The percent of scans the orangutans were observed inactive across the phases of this study (Lockdown vs Visitor).

3.2.2 Self-directed displacement behaviours

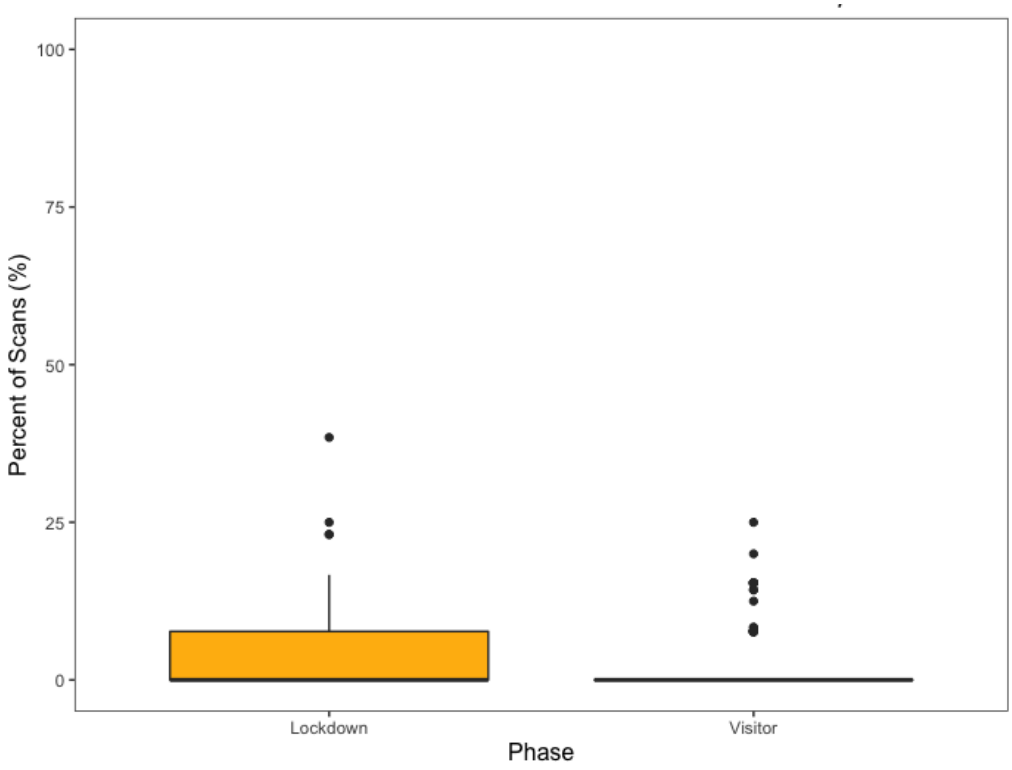


Figure 6. The percent of scans the orangutans were observed performing self-directed displacement across the phases of this study (Lockdown vs Visitor).

As shown in Figure 6, the orangutans did not significantly increase (t (245.74) = –1.263, p = .21) the amount of time they spent performing self-directed behaviours. Because displacement behaviours were rarely seen, it is necessary to analyse the increase of frequencies in these behaviours. The orangutans increased (t (234.60) = 3, p = .003) their rates of self-directed behaviours by 0.0097 events per minute during the visitor introduction phase when compared to the lockdown phase (Figure 7). However, from a practical perspective, the effect size is too small (95% CI [0.003,0.016]) for this to be a meaningful difference. When these rates are thought of as events per 100 minutes, an increase of ~1 bout of self-directed behaviour does not seem to be indicative of elevated arousal levels. In a study conducted on zoo-housed orangutans, self-directed behaviour rates ranged from 1–7 per 60 minutes (Perdue et al., 2012). This is more than twice the average rates of self-directed behaviours performed by the Toronto Zoo orangutans even during visitor introduction (Figure 7). Furthermore, when taken together with the lack of significant increase in percent of time spent performing self-directed behaviours, it seems that the orangutans simply had more bouts that were shorter in duration.

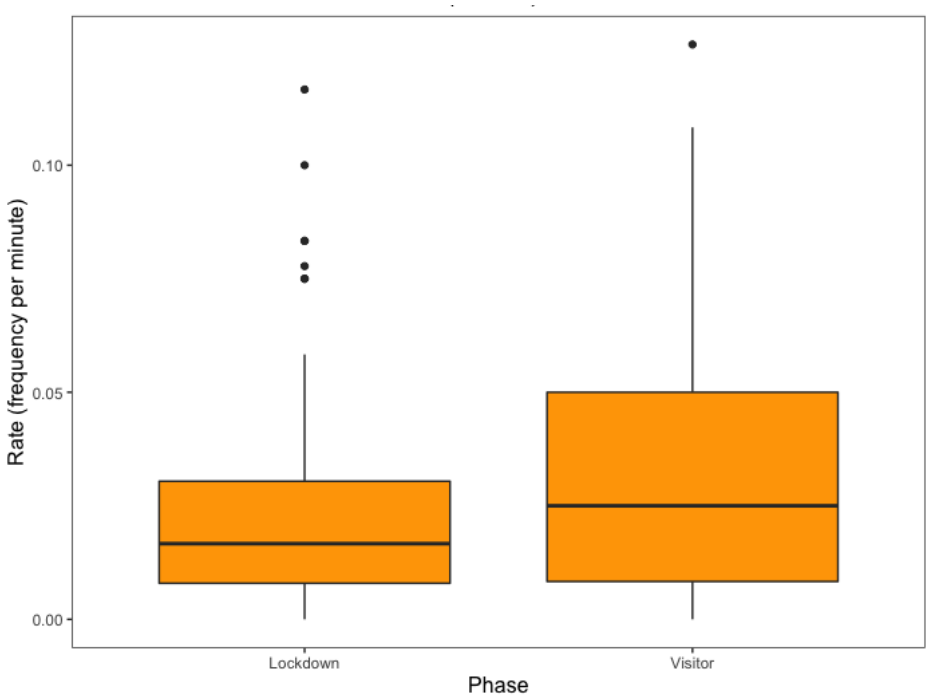


Figure 7. The per minute rate the orangutans performed self-directed displacement across the phases of this study (Lockdown vs Visitor).

3.2.3 Object-directed displacement behaviours

Meanwhile, only two (Puppe and Sekali) of the six orangutans performed displacement behaviours directed towards objects. For both of these individuals, the frequencies of these behaviours were even rarer than self-directed behaviours. These behaviours were also very idiosyncratic (fabric tearing for Sekali and head slamming into a pile of blankets for Puppe). As shown in Figures 8 and 9, neither Puppe (t (39) = 0.54, p = .59) nor Sekali (t (49) = 0.62, p = .54) respectively showed any change in the rates of these behaviours when visitors were introduced.

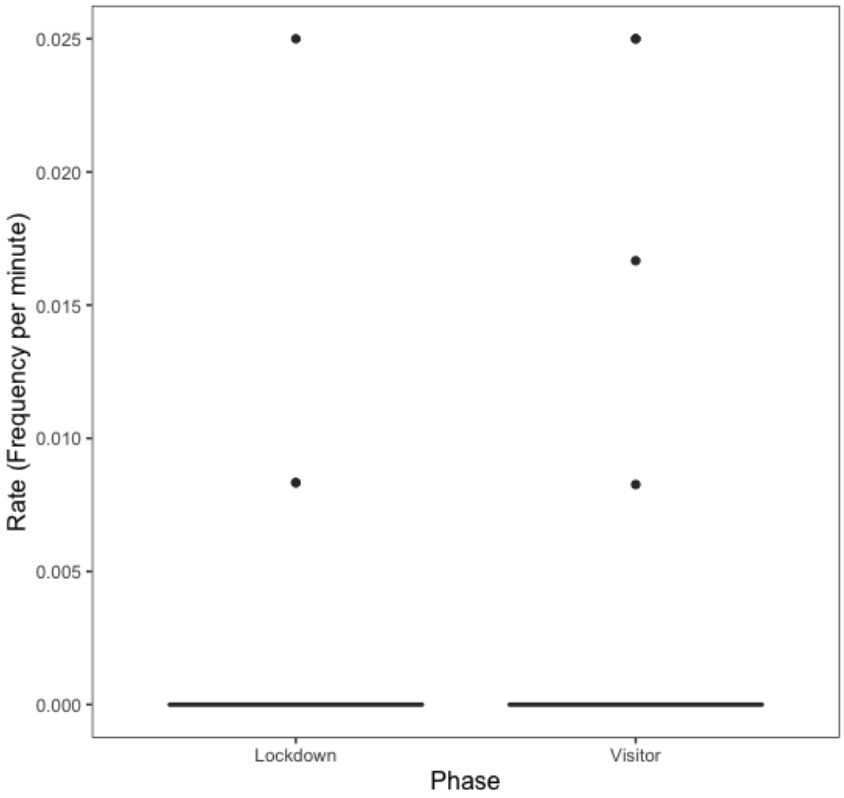


Figure 8. The per minute rate of Puppe's performance of object-directed displacement (Head slamming) across the phases of this study (Lockdown vs Visitor).

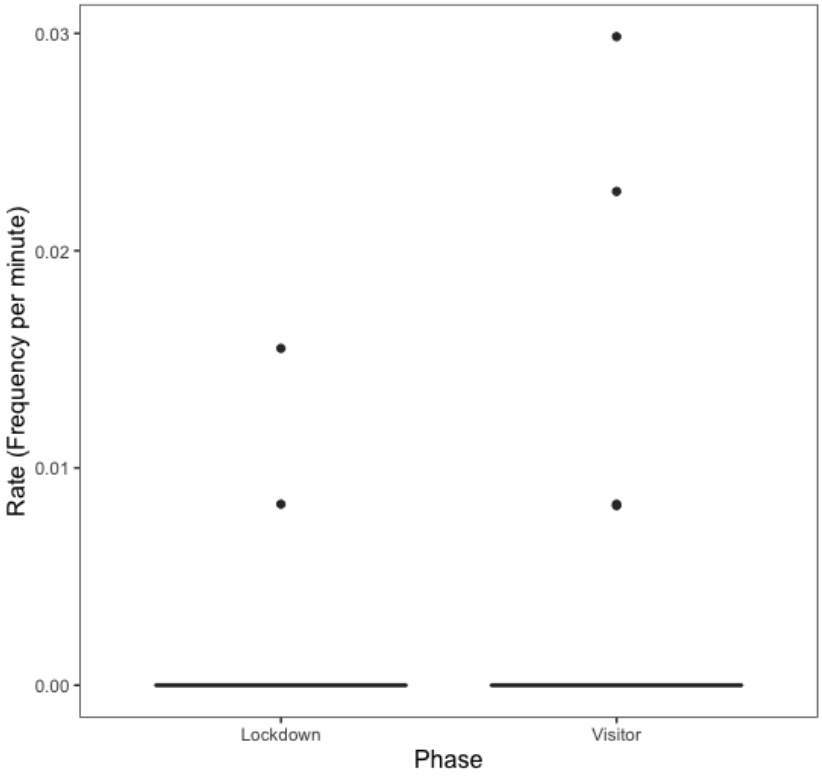


Figure 9. The per minute rate Sekali performed object-directed displacement (fabric tearing) across the phases of this study (Lockdown vs Visitor).

3.2.4 Displacement behaviours towards conspecifics

Displacement could also be directed towards conspecifics. Although orangutans in the wild are usually solitary and follow a fusion-fission system, they may be found in dyads as a mother-offspring pair or a consort pair. The Toronto Zoo orangutans were in a similar structure at the time of the study, with two dyads (Sekali-Budi and Ramai-Jingga). This setup provided an opportunity for arousal to be displaced as agonistic behaviours in these animals. As seen in Figure 10, Sekali's agonistic behavior rate did not significantly change (t (49) = –0.169, p = .87) towards Budi, and Budi did not significantly increase (t (47) = 1.379, p = .17) his rate of agonistic behaviours towards Sekali when visitors were introduced (Figure 11). As for the mother-daughter pair Ramai and Jingga, only Jingga showed an increase in per minute rate of agonistic behaviour towards Ramai when visitors were introduced (Jingga, t (39) = 2.44, p = .02; Ramai, t (42) = 0.54, p = .22). Jingga increased her mean per minute agonistic behaviour rate (Figure 12) during the visitor introduction phase by 0.006 events during the lockdown phase. In other words, if each observation period ran for 1000 minutes, on average we would see Jingga perform 6 more agonistic behaviour events during visitor introduction than during lockdown. Practically, this increase is negligible (95% CI [0.003,0.016]) and likely does not indicate increased arousal especially given that the observed behaviours involved refusal to share food with her mother, Ramai. Additionally, it is important to note that the behaviour, particularly the choice of location of orangutans in dyads are not necessarily independent. The mother and daughter pair (Jingga-Ramai) spent more time together (67.57% of scans) than the consort pair (Budi-Sekali) (39.89% of scans).

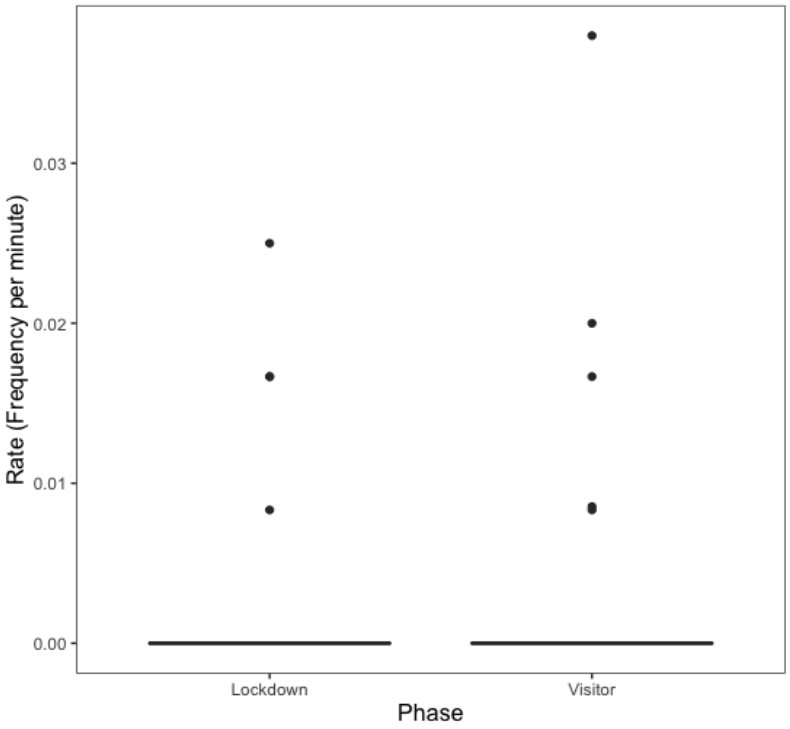


Figure 10. The per minute rate Sekali performed agonistic behaviours towards Budi across the phases of this study (Lockdown vs Visitor).

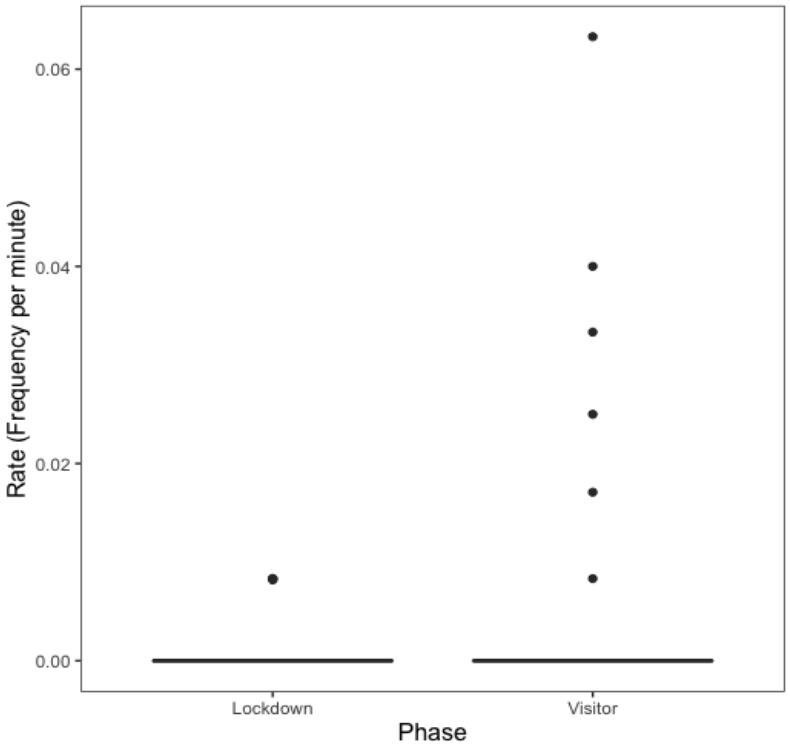


Figure 11. The per minute rate Budi performed agonistic behaviours towards Sekali across the phases of this study (Lockdown vs Visitor).

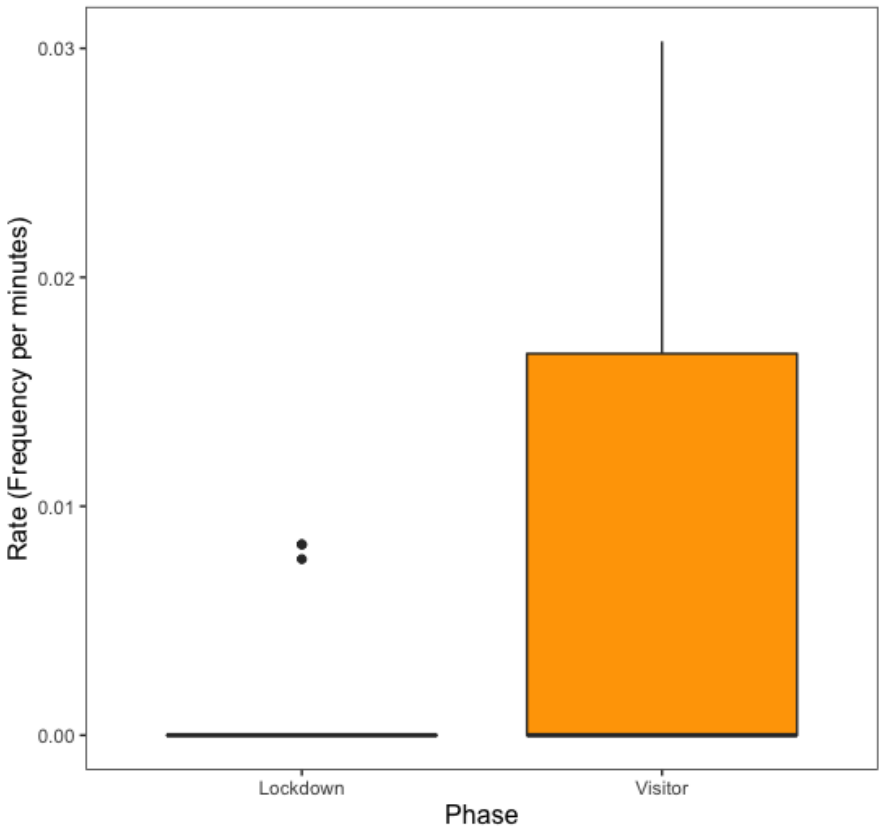


Figure 12. The per minute rate Jingga performed agonistic behaviours towards Ramai across the phases of this study (Lockdown vs Visitor).

3.2.5 Agitated movement

The last behavioural indicator of arousal is agitated movement. Only Puppe was excluded from this analysis due to her advanced age and slow movement. The orangutans did not significantly change (t (246.12) = 0.052, p = .96) the amount of time spent in the state of agitated movements (Figure 13). Similarly, the frequency of agitated movements (another rarely seen behaviour) did not significantly change when visitors where introduced (t (193) = –0.224, p = .82) (Figure 14).

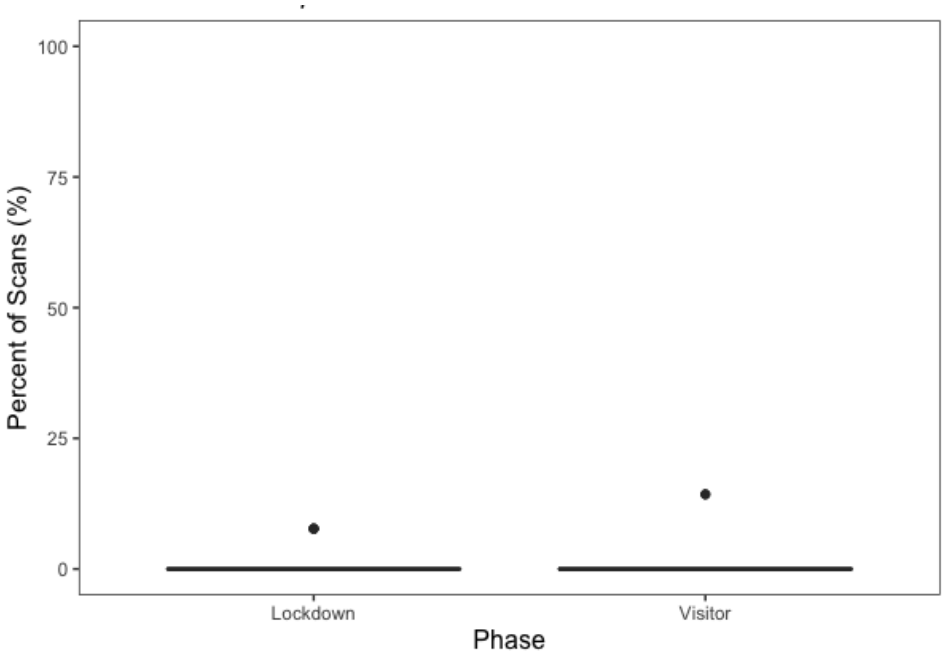


Figure 13. The percent of scans the orangutans were observed performing agitated movements across the phases of this study (Lockdown vs Visitor).

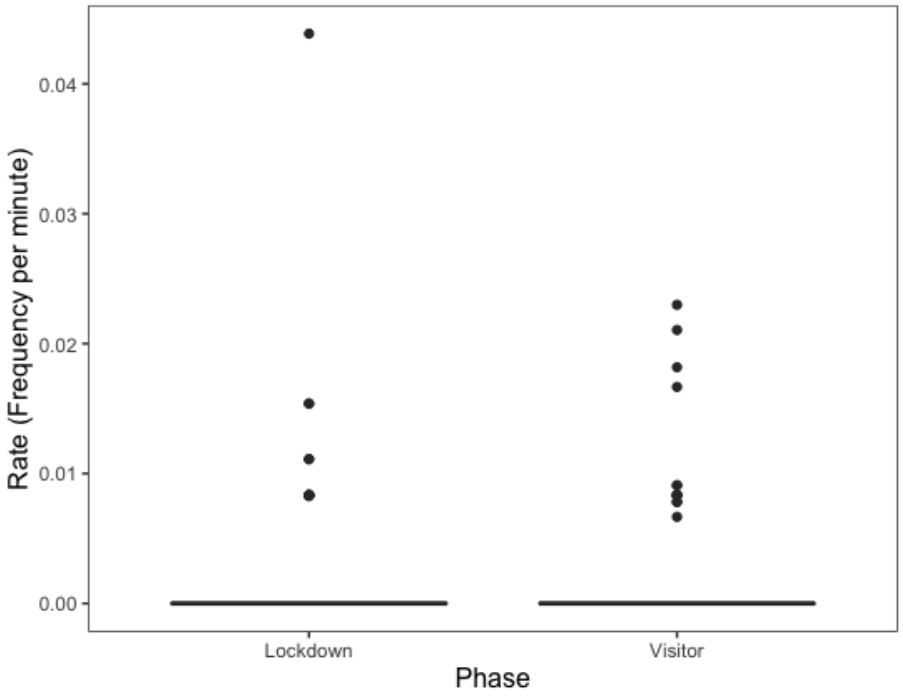


Figure 14. The per minute rate the orangutans performed agitated movements across the phases of this study (Lockdown vs Visitor).

3.2.6 Fecal consistency

The behavioural evidence indicate that the orangutans effectively coped with the introduction of the visitors. However, it is also possible that the behavioural measures were not sensitive enough. Hence, it is still necessary to explore the physiological signs of arousal of the orangutans due to the visitor introduction. I analysed the difference in frequencies of the orangutans' bowel movement issues between the lockdown and the visitor introduction phase.

Of the fecal samples collected during lockdown 40.87% were abnormally loose or solid; Whereas, during the visitor introduction phase these abnormal stools comprises 34.74% of the fecal samples (Figure 15). The odds of seeing stools during the visitor introduction phase with abnormal consistency was multiplied by 0.79 which is not statistically significant ($z = –0.71$, $p = .48$). Being on exhibit did not significantly increase the likelihood of seeing abnormal fecal consistency (*Odds ratio* = 0.59, z = –1.45, $p = .15$). In other words, there was no evidence from fecal consistency scores that indicate prolonged arousal associated with the visitor reintroduction (χ^2 (2) = 2.92, $p = .23$).

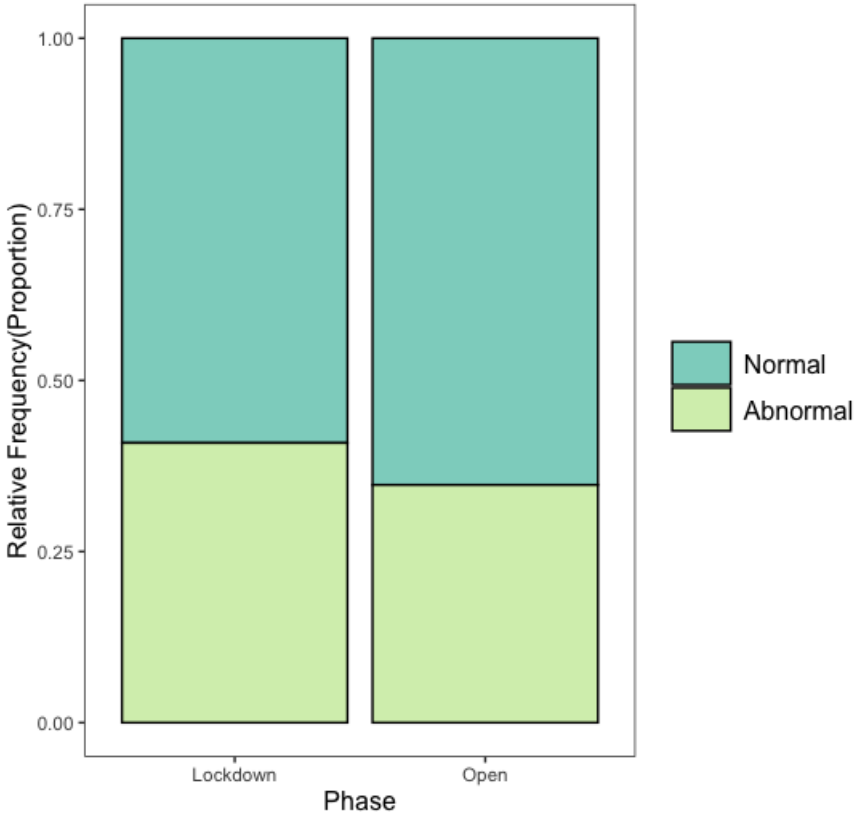


Figure 15. The percent of normal vs abnormal fecal consistency scores across the phases of this study (Lockdown vs Visitor).

3.3 Other humans: the effect of keeper presence

As discussed above, the lack of change in the amount of space the orangutans used reflects their evaluation that the visitor introduction was not aversive. Nonetheless their consistent preference of the back platform area raised the question whether these orangutans had learned to sit there in order to avoid visitors. The orangutans' choice to not hide when visitors were reintroduced is evidence against the idea of learnt constant aversion. Furthermore, there is evidence for an alternative explanation – that is, they preferred the back platform to be close to where the keepers are. As shown in Figure 16 there was a strong linear relationship between the per minute rate of keeper presence and the per minute rate of keeper directed

behaviour. Regardless of the phase (i.e. lockdown vs visitor reintroduction), each time the keepers increased their frequency of visits, there was a 0.27 increase in rate of keeper directed behaviour (t (237) = 9.21, p < .001). The linear model including both the phases and the keeper presence rate explains a more significant amount of variability in keeper directed behaviour than just individual differences alone (χ^2 (2) = 75.06, p < .001). This effect is also practically significant (95% CI [0.21,0.33]). If the keepers were present at the public area 10 visits more than usual during an observation period, the orangutans increased their keeper directed behaviours by 2–3 events more within a period of 10 minutes. This correlation suggests how important the presence and behaviour of the keepers are for the orangutans.

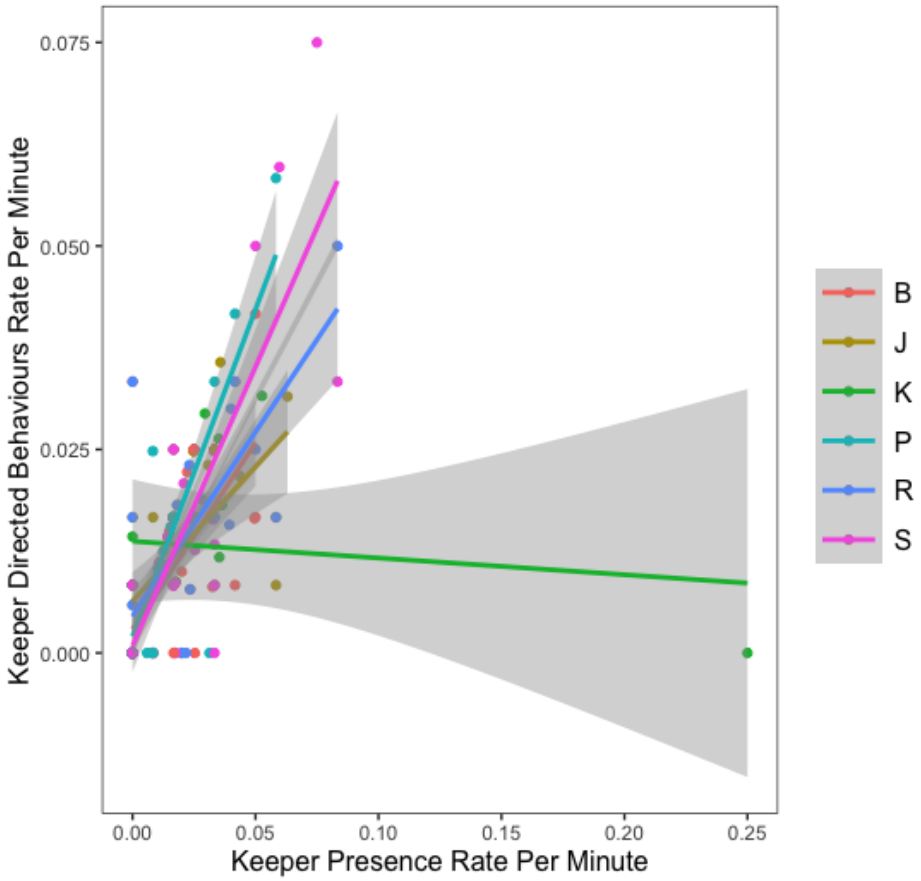


Figure 16. The relationship between the per minute rate of keeper-directed behaviours by the orangutans and the rate of keeper visits within the proximity of the exhibit. The initials represent each orangutan (B = Budi, J = Jingga, K = Kembali, P = Puppe, R = Ramai, S = Sekali).

Interestingly, the orangutans did not actively search for the keepers when the keepers were in their vicinity less frequently. The relationship between the rates of keeper presence and scanning behaviour was weak (Figure 17). Regardless of the phase, every time the keepers increased their frequency of visits, the orangutans performed 0.04 more bouts of scanning per minute (t (237) = 0.06, p = .96). However, this model does not do significantly better at

explaining the variability in scanning more than the existing individual differences (χ^2 (2) = 0.41, p = .82). These results are consistent with the fact that the orangutans already chose to spend most of their time at the place where the keepers occasionally appeared in order to give them enrichment. Hence, they did not need to actively search for the keepers but only needed to pay attention to them when they were in the vicinity of the orangutan exhibit.

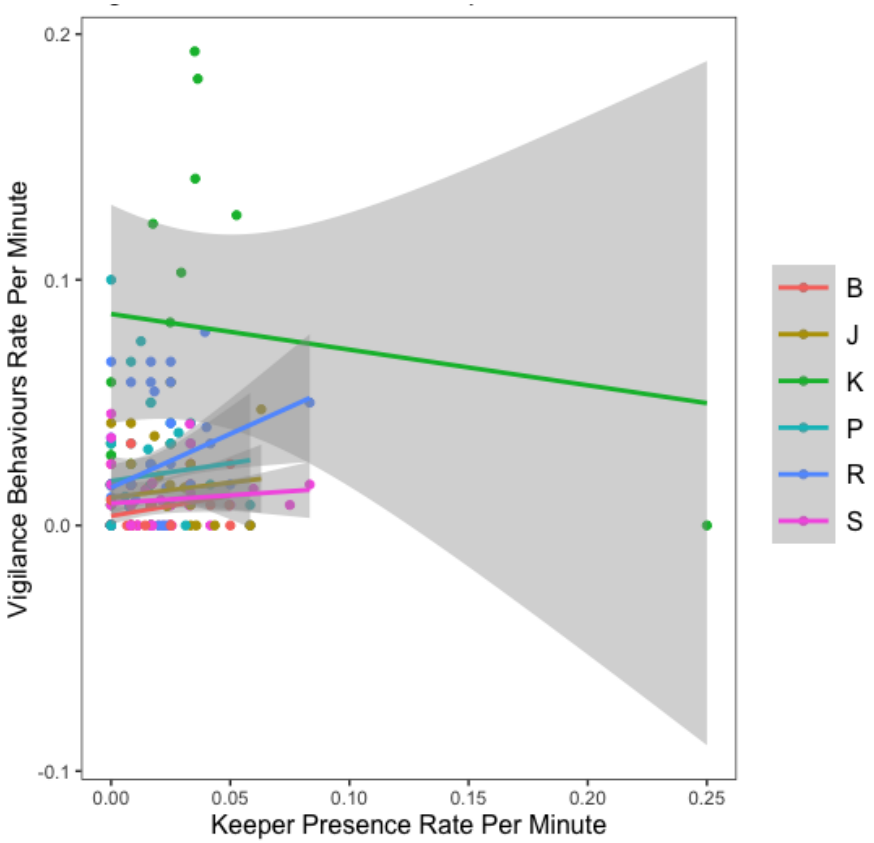


Figure 17. The relationship between the per minute rate of vigilance behaviours (i.e., scanning) by the orangutans and the rate of keeper visits within the proximity of the exhibit. The initials represent each orangutan (B = Budi, J = Jingga, K = Kembali, P = Puppe, R = Ramai, S = Sekali).

4. Discussion

The COVID-19 lockdown measures have affected the lives of people and wildlife alike. These lockdown measures allowed us to study the relationship of visitor presence with the welfare of zoo-housed non-human primates as a natural experiment, by taking advantage of an unprecedented opportunity to study these animals with and without the presence of visitors. The purpose of my thesis was to understand whether visitor reintroduction negatively affected the welfare of Sumatran orangutans at the Toronto Zoo. The findings indicate that for this group of orangutans, their welfare states were not negatively affected by the reintroduction of visitors after a lockdown. My thesis has two key groups of findings: that there was no change in physical space use when visitors were introduced and that there were no changes in behavioural and physiological indicators of arousal. The results on their physical space use suggest that these orangutans did not avoid the visitors, suggesting that the orangutans did not find the presence of visitors aversive. Similarly, there was no change in "rest and digest" behaviours, displacement behaviours (e.g., self-directed, agonistic behaviours, and object directed), and fecal consistency ratings when visitors were introduced. Because these indicators change when there is high arousal (Caine, 2017; Murakami et al., 2017; Troisi, 2002; Welgan et al., 1995), the results suggest that there was no change in arousal associated with visitor reintroduction. Given that visitor reintroduction did not fit the two-part definition of stress – that is, stress is high arousal with aversive behaviour (Kim & Diamond, 2002) – the findings indicate that the orangutans were not stressed by the reintroduction of visitors after lockdown ended. Welfare is defined as the capacity of the animal to cope (Broom, 2011), and stress is a manifestation of the inability to cope through changes. Therefore, the findings do not support the hypothesis that the visitor reintroduction negatively affected the welfare of the orangutans at the Toronto Zoo.

The findings stand in contrast with some of the findings of other studies done on visitor effects in orangutans in other zoos. Most studies on zoo-housed orangutans have reported various changes in behaviour and physiological measures as visitor numbers increased throughout the day (Amrein et al., 2014; Birke, 2002; Choo at al., 2011; Sherwen & Hemsworth, 2019). When compared to my thesis, these studies measured visitor numbers/ crowd size instead of the complete absence of visitors. Because visitor numbers fluctuate at fixed time periods throughout the day, the reported changes could have also reflected confounding variables like scheduled keeper talks, timing of feeding and cleaning, and even internal diurnal cycles of the orangutans that participated. Additionally, of the studies that reported behavioural changes, only Amrein and colleagues (2014) reported an increase in

arousal indicators with increasing visitor numbers. By contrast, in my study, the orangutans did not show an increase in these measures when visitors were introduced. However, given the relationship of daily routine activities (e.g., feeding times, cleaning, keeper talks), and diurnal cycles with visitor numbers, the increase in arousal that Amrein and colleagues (2014) reported could have been due to positive events. Without evidence of aversive behaviours, it is difficult to disambiguate positive anticipation from stress. When the confounds of daily routine activities were dissociated with visitor numbers as in the case of my thesis, the previously reported increase in arousal disappeared.

Meanwhile, of the previous studies of visitor effects on orangutans, only Bloomfield and colleagues (2015) experimentally manipulated the visibility of the visitors. Again, however, their results stand in contrast to the results of my thesis. The orangutans in their study approached the viewing glass when visitors were visible. The orangutans in my study remained on the back platform and did not change their exhibit use. A possible explanation for this difference is that the orangutans at the Toronto Zoo paid more attention to the keepers than the orangutans who participated in Bloomfield and colleagues' (2015) study, It is difficult to make the comparison on welfare effects, because Bloomfield and colleagues (2015) did not report the attention the orangutans directed towards their keepers. Additionally, Bloomfield and colleagues (2015) did not report behavioural or physiological indicators of arousal. This missing piece of evidence makes it difficult to interpret whether those animals were fully able to cope with visitors or were stressed. Because we do not know how well the orangutans were able to cope in the previous study, we do not know how much their welfare was affected by the visitors. A fuller picture that combines multiple measures is necessary if we are to understand the effects of visitors on welfare (Sherwen & Hemsworth, 2019). This is particularly the case when we measure stress, which requires both measures of aversive behaviours and arousal (Kim & Diamond, 2002). Otherwise, comparing the findings of the studies regarding the welfare effects of visitors would repeatedly fall into subjective interpretations that barely scratch the surface of welfare. This is because the measured changes do not really pertain to anything related to welfare. As it stands, among the studies of visitor effects on zoo-housed orangutan welfare, only my thesis combined both information about arousal and aversive behaviours.

As mentioned above, both the way visitor presence was manipulated and the characteristics of the environment where research was done are important in contextualising the interpretation of the findings regarding visitor effects on welfare. Among the studies done in the context of the COVID-19 lockdowns, mine found very similar findings – that is, no

behavioural or physiological changes were associated with the introduction of visitors (e.g., Edes et al., 2022; Krebs & Watters, 2022; Masman et al., 2022; Williams et al., 2022). The welfare effects of human-animal relationships are often conceptualised as either positive, negative, or neutral. In the case of the COVID-19 lockdowns when the context of other daily routine variations was dissociated with visitor presence, the effects associated with visitors were neutral among various species. Krebs and colleagues (2022) attempted to reconceptualise it with the idea that all positive, negative, and neutral effects can happen at once in relationships between visitors and zoo-housed animals. They studied zoo-housed mammals (reticulated giraffes, meerkats, and prairie dogs) and birds (Chilean flamingos) that were all situated at areas of their zoo that had heavy visitor traffic. Their multi-species study (which focused on visitor numbers throughout the day as opposed to presence or absence) found that moderate level of visitor numbers was associated with reduced frequencies of self-directed behaviours. They argued that the moderate number of visitors signalled the absence of predators; something they called the "dither effect" (Krebs et al., 2022). They, however, lumped the visitors and staff in their counts and did not account for the confounding effect of keeper presence. It is possible that the effects of visitors were neutral and what they found in their study reflected the welfare effects of other daily routine variations or other external factors that simply fluctuated with visitor presence (Goodenough et al., 2019). For example, similar to what was illustrated by my findings, the animals involved in their study could have been more attuned to the keeper routine than visitor presence. The routine of the keepers could have coincided with either higher or lower visitor numbers. The findings of my thesis along with those of other studies of visitor effects during COVID-19 lockdowns confirm the assertion of Goodenough and colleagues (2019): that for some species, other external factors (e.g., weather, time) better explain behavioural changes commonly associated with visitors. Hence, the complicated dither effect model (Krebs et al., 2022) may simply be accounting for the presence of these confounds. Reinventing the wheel may have not been necessary to understand the welfare effects of visitor human animal relationships.

Interestingly, the findings do suggest the potential to explore the dither effect in orangutans directed towards their conspecifics. The original dither effect study was done on fish in aquarium. Dithering happens when a fish reduces fear response to certain stimuli when a less reactive conspecific is added to the tank (Barlow, 1968). This is especially important for the mother and daughter pair (Jingga-Ramai) who spent a majority of their time in the same area. I do not have evidence of copying of coping behaviours and responses among the paired orangutans in this study. However, the evidence on social transmission of behaviours that range

from tool use to nest building habits in wild orangutans suggests that orangutans have the capacity to copy and learn behaviours socially (Dindo et al., 2011; Russon et al., 2007; van Schaik et al., 2003). Therefore, learning behavioural reactions to various stimuli socially is likely for orangutans. Given that dither effects are not explored widely in settings outside of fish husbandry (Jordan & Burghardt, 1986), there is a gap to be filled in the understanding of the dither effect in other animals. However, the number of orangutans that participated in my thesis is small. Additionally, pairing orangutans randomly is difficult due to specific husbandry regulations (e.g., around genetics and breeding) and individual preferences by the orangutans themselves. Hence, testing for this effect was not feasible. Nonetheless, this could be a potential direction to explore for captive orangutan welfare.

Likewise, while considerable research has been done on visitor effects on animals in human care, it is important to also understand the effects of their caregivers, who are a consistent daily presence throughout their lives. Orangutans in human care approach novel items more frequently than orangutans in the wild (Forss et al., 2015). Forss and colleagues (2015) argue that orangutans in human care are often given novel items that do not have negative consequences. They further assert that because of this positive interaction, the orangutans tend to trust their keepers. In the case of the orangutans at the Toronto Zoo, the evidence suggests that the keepers also affect their behaviours. When taken with the evidence on the use of space, the orangutans not only approach their keepers, they also direct their attention to them, suggesting they view them positively. It is also important to note that keepers were present in the orangutans' lives throughout the lockdown and visitor reintroduction phase and thus are a constant presence for these animals. It is not surprising, then, that keeper presence has the potential to affect welfare more than visitor presence. This provides an opportunity for more research particularly on the effects of keeper presence in reducing aversion to other stimuli. Knowing that orangutans generally have positive interactions with their keepers also opens up the possibility of varying the place and time of keeper routine to coax orangutans to explore more of their environments; something that would help with their physical health.

5. Limitations

The limited sample size means that the individual differences of the orangutans that participated in my thesis is a limitation to the generalisability of my findings. Likewise, the context of the setting and type of possible interaction with visitors are also limitations. For one, the participating orangutans were mostly captive born with the exception of Puppe. For the most part, they were all from accredited North American zoos where human interaction is limited to watching. Within this context, visitors may have neutral consequences and therefore evoke neutral reactions from orangutans. As was apparent in the discussion, the history of consequences of human interaction with a specific orangutan may affect how they react to visitors. Obviously, an orangutan that was poached from the wild would have experienced negative consequences and would have reacted differently. Interestingly, this was not the case for Puppe who was wild born. However, she had spent many decades under human care since moving to the Toronto Zoo. Nonetheless, it would be interesting to replicate the findings of my thesis in orangutans in sanctuaries and rescue centres.

Another further limitation to my thesis is scale, reliability, and validity of the measures used to indicate arousal. Because there was only one observer due to the design of the study and the lockdown restriction, there was no inter-observer reliability for the behavioural measures. Meanwhile, in terms of validity, the most commonly used behavioural indicator of negative welfare state in primates is self-directed displacement behaviour (Troisi, 2002). This behaviour has been shown to decrease when doses of the anxiolytic Lorazepam are administered to laboratory macaques (Schino et al., 1991). However, the scale at which changes in frequencies of self-directed behaviours are indicative of high arousal does not exist. As highlighted by my findings, if a small but statistically significant change in the frequency of self-directed behaviour occurs, would that warrant concern? Would that be meaningful to the orangutans? While the macaques in Schino and colleagues' study (1991) performed around 10–20 bouts of self-directed behaviours per hour, other species behave differently. Wild chimpanzees perform this behaviour less than macaques (Botero et al., 2015) and some studies of zoo-housed orangutans show that orangutans perform even fewer self-directed behaviours (Perdue et al., 2012). My findings highlight that the scales need further investigation. Additionally, the measures of self-directed displacement do not correlate with measures of arousal like cortisol levels (Amrein et al., 2014). However, Amrein and colleagues (2014) found that the age of the individuals affect the arousal response such that younger Bornean orangutans respond to increasing visitor numbers with an increase in cortisol levels while older orangutans did so with an increase in frequencies of self-directed behaviours. To my

knowledge, there is also no study exploring the correlation between self-directed behaviours and fecal consistency. Thus, the validity of these measures of arousal is in question. Because I needed to use multiple measures of arousal to capture multiple possible manifestations of arousal, my thesis highlights the need for more validation studies regarding these measures. Nonetheless, because I used multiple measures in this thesis, I was able to account for multiple possible ways arousal could have manifested in orangutans.

Additionally, I used fecal consistency scores as a measure of physiological arousal. Usually, physiological arousal in animals is measured non-invasively using levels of cortisol in feces or urine (Touma & Palme, 2005). This is meant to reflect the activities of the hypothalamic-pituitary-adrenal axis which is active during the stress or arousal response. Fecal consistency scores are not commonly used to indicate the physiological stress response. Nonetheless, in humans, fecal consistency scores are associated with diet and stress levels, particularly with stress hormones (Lemay et al., 2021). Given that the stress response is highly conserved across species, it is reasonable to use fecal consistency scores as a proxy to cortisol levels. The diet of the orangutans may have affected their fecal consistency scores. However, the diet of the orangutans remained consistent throughout the study since their food was measured for nutrition maintenance. Therefore, if any changes in their fecal consistency scores occurred during the study, it would not have been due to diet. Nonetheless, my thesis shows the potential use of fecal consistency scores as an alternative to the more labour intensive and expensive use of fecal cortisol levels to measure physiological arousal.

Lastly, even though the lockdown provided a rare opportunity as a natural experiment to reduce visitor numbers to zero for weeks, causal relationships may not be inferred from the findings of this study. The lockdowns were unpredictable and did not allow for a reversal wherein guests were not allowed following weeks of exposure to visitors. This lack of reversal introduced the confounding variable of order effects. While the orangutans have been exposed to visitors all their lives, visitors tend to fluctuate across the year for the Toronto Zoo. The study happened between May to August 2021 which would have been the yearly peak of visitor presence. Hence it would have been possible that the orangutans were already stressed in anticipation of visitors; Thus, the indicators would not have shown any difference between lockdown and visitor reintroduction phase (i.e., ceiling effect). A reversal would have suggested that even in a non-peak season, the indicators of arousal and aversive behaviours were not any different to the visitor reintroduction phase. However, given that the average levels for the indicators across the phases of the study were close to zero, it is unlikely that this was a case of ceiling effect.

6. Conclusion

In general, visitor presence after the lockdown had a neutral relationship with the welfare measures of the orangutans at the Toronto Zoo. The difference in the dynamics between visitors and keepers is interesting. While both keepers and visitors are humans, the relationship of welfare measures with keeper presence is positive, whereas the relationship with visitor presence is neutral. It becomes even more impressive when we consider that in the wild, there is evidence of human predation towards orangutans (Campbell-Smith et al., 2012; Delgado & van Schaick, 2000; Drake, 2015; Marshall et al., 2006; Meijaard et al., 2011; Nijman, 2017). This explains the physiological arousal found by Muehlenbein and colleagues (2012) among wild orangutans when they were exposed to visitors. These differences in the reaction of the orangutans highlight the importance of differences in the consequences of interactions that each group has with the orangutans. Positive consequences beget positive reactions and so on and so forth. The type of interactions the guests at the Toronto Zoo were allowed was neutral and limited to watching or the occasional tapping on the glass. By contrast, Choo and colleagues (2011) found that when visitors at Singapore Zoo were holding food and were actively engaging with orangutans, the orangutans were more likely to approach the visitors than when the visitors were passive and just taking photos. The orangutans at Singapore Zoo could swing above visitors on low overhanging lines making the barrier between the visitor and orangutans less apparent. However, this does suggest that in a context of positive association with food and visitors, orangutans could show positive reactions to visitors. I am not suggesting that guests should actively feed orangutans as this could potentially affect welfare negatively through disease transmission and conspecific aggression. Simple respect towards the animals' space would even suffice. However, the evidence does point to the potential welfare benefits of changing human behaviour, whether visitors' or keepers', towards behaviours that bring positive consequences to orangutans and perhaps other zoo-housed animals. Hence, more research on human-animal interactions in zoos should focus on the effects of human behaviour as opposed to simple presence and absence, numbers, and noise level. Animals change and cope with the challenges that their environment presents them (Broom, 1986, 2011; Dawkins, 1983, 1988, 2017). For animals in human care, their challenge is to have their lives be fully intertwined with ours. We are part of their environment. We, as humans, have the potential to make coping much easier for animals under our care.

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