Manchester
Metropolitan
University

Hashmi, Anita and Sullivan, Matthew (2020) The visitor effect in zoo-housed apes: the variable effect on behaviour of visitor number and noise. Journal of Zoo and Aquarium Research, 8 (4). pp. 268-282. ISSN 2214-7594

Publisher: European Association of Zoos and Aquaria

DOI: https://doi.org/10.19227/jzar.v8i4.523

JZAR www.jzar.org JOURNAL OF ZOO AND AQUARIUM RESEARCH

JZAR Research article

Research article

The visitor effect in zoo-housed apes: the variable effect on behaviour of visitor number and noise

Anita Hashmi[1] **and Matthew Sullivan**[1]

[1]Manchester Metropolitan University, All Saints Building, All Saints, Manchester M15 6BH

Correspondence: Anita Hashmi, email; anita.hashmi@stu.mmu.ac.uk

Keywords: apes, behaviour, visitor effects, welfare

Article history:
Received: 11 Feb 2020
Accepted: 06 Oct 2020

Abstract

Human visitors have the potential to impact heavily upon the welfare of zoo-housed animals, and the study of the effect has become an established research area in the modern zoo. This effect can be caused not just through the presence of visitors, but also through their behaviour. This study sought to test the hypothesis that visitor number and the associated noise level significantly affected the behaviour of three zoo-housed primate species. This was studied through behavioural observations and measurements of visitor numbers and noise levels around enclosures, as primate species are particularly sensitive to large, noisy crowds of zoo visitors. Changes in behaviour relating to visitor number and noise levels were investigated on a species and individual level. Noise levels had a significant positive relationship with visitor number, and both factors had significant positive and negative effects on stereotypic, locomotory, inactive and feeding behaviours on an individual and species level. However, levels of individuals sitting with their back to the window was unaffected by visitor number or noise. Individual and species differences were seen in reactions to the visiting public, emphasising the complex nature of the study of the visitor effect. The increase in stereotyping and clinging behaviours, and decrease in inactivity suggest a potential negative influence on the welfare of these primates. The mixed results reinforce the notion that the visitor effect is moderated and influenced by many factors, such as husbandry and personality. The current study highlights the need for off show areas for captive primates, and the importance of considering individual differences when attempting mitigation of unwanted behaviours.

Introduction

One prevalent factor of life for zoo-housed animals is visitors to the institution which houses them. Since the 1980s, the study of the visitor effect has become an established research area (Fernandez et al. 2009; Collins and Marples 2016). Visitors can present as a welfare issue that is not easily remedied. Two main hypotheses exist regarding zoo visitors: 'visitor attraction', whereby visitors are more attracted to more active animals (Mitchell et al. 1992a), and 'visitor effect', whereby the presence of visitors changes animal behaviour. The 'visitor effect' exerts differing influences dependent on various factors. Visitors can be enriching for some species (Markowitz et al. 1981; Moodie and Chamove 1990; Hosey 2000; Hosey 2005) or have no effect (Fa 1989; Mather 1999; Collins et al. 2017). Interestingly, the COVID-19 pandemic has prompted reports of animals 'missing' visitors. However, visitors may be defined as a 'stressful influence' (Hosey 2000) and detrimental to welfare. This effect can cause negative behavioural responses in zoo-housed animals, for example, decreased activity (Chamove et al. 1988; Mitchell et al. 1992a; Wells 2005), increased aggression (Chamove et al. 1988; Mitchell et al. 1991; Blaney and Wells 2004; Wells 2005; Kuhar 2008; Collins and Marples 2016).

The visitor effect is multifaceted. Hosey (2000) argues that primates are particularly sensitive to the visitor effect, and the majority of previous literature suggests a stressful influence; a mix of positive, neutral and negative results have been noted in non-primates (Fernandez et al. 2009). Varied responses to human presence and behaviour have been observed across

https://doi.org/10.19227/jzar.v8i4.523

Table 1. All individuals included in behavioural observations.

Species	Names	Sex	Age at beginning of study
Gorilla gorilla gorilla	Bukavu	M	20
Gorilla gorilla gorilla	Miliki	F	23
Gorilla gorilla gorilla	Njema	F	24
Gorilla gorilla gorilla	Meisie	F	7
Gorilla gorilla gorilla	Moanda	M	3
Gorilla gorilla gorilla	Makari	M	6 months
Pongo pygmaeus	Ramon	M	19
Pongo pygmaeus	Vicky	F	33
Pongo pygmaeus	Cherie	F	21
Pongo pygmaeus	Summer	F	15
Pongo pygmaeus	Jingga	F	8
Hylobates pileatus	Chamoa	M	16
Hylobates pileatus	Ivy	F	29
Hylobates pileatus	Dobby	M	3
Hylobates pileatus	Baby	M	4 months

primates (Chamove et al. 1988; Clark et al. 2011). Suggestions for this discrepancy include social structure (Hosey 2005) and body size (Chamove et al. 1988); however, there is no clear evidence for the cause of these differences. Furthermore, questions persist about the influence of age on the effect of visitor presence and noise levels, exemplified by studies including infant-specific behaviours (e.g., Birke 2002; Cheyne 2006; Collins and Marples 2016). Sex, environment and personality may all influence the visitor effect and its expression. Environment is a complex variable, as it differs significantly across institutions. However, a key requirement for reducing negative reactions to visitors is seemingly free access to private areas. Blaney and Wells (2004) observed reduced aggression and abnormal behaviours in gorillas after the provision of a camouflage net, which reduced direct visual contact with visitors. Similarly, the use of privacy screens reduced negative vigilance behaviour in a second group of gorillas (Clark et al. 2011) and aggression in capuchins (Sherwen et al. 2015). Furthermore, Bornean orangutans displayed increased avoidance behaviour at times of high visitor density (Birke 2002). It is unclear whether the influential factor is privacy or the choice to use it. When given the choice to use private areas, polar bears performed less stereotypic pacing and increased social play (Ross 2006), and pandas showed lower levels of behavioural agitation (Owen 2004). Freedom of choice reducing visitor stress behaviours has also been seen in orangutans: the provision of choice led to infrequent observations of stereotypic, abnormal and aggressive behaviours (Bloomfield et al. 2015). Additionally, visitor behaviour also appears to exert differing effects: passive audiences do not elicit the same response from captive primates as active audiences (Hosey and Druck 1987; Mitchell et al. 1992a; Birke 2002).

Previous studies have established certain behaviours as stress indicators. Stereotypic behaviours, defined as "repetitive behaviours that are abnormal when compared to the animal's natural behaviour patterns" (Wielebnowski 1998), are an indicator of stress or an inability to cope with a stressor. In primates, common stereotypies include self-harming, for example, scratching and mutilation (Cooke and Schillaci 2007; Hosey and Skyner 2007; Carder and Semple 2008), and atypical ingestion behaviours such as coprophagy (Bloomsmith et al. 2007). Regular display of these can allude to underlying welfare issues. Further situation-specific behaviours include visitor avoidance, animals sitting facing away from visitors (Collins and Marples 2016), and increased aggression (Chamove et al. 1988; Mitchell et al. 1991; Kuhar 2008; Bortolini and Bicca-Marques 2011), and locomotion (Chamove et al. 1988; Mitchell et al. 1992a; Wells 2005). Many of these behaviours have been treated as indications of fear of humans in domestic animals (Hemsworth et al. 2018) and of a negative welfare state (Botreau et al. 2007; Mellor et al. 2009; Hosey 2013). Furthermore, it has been suggested that relatedness to humans may influence behavioural reactions to visitors. Direct eye contact is a threatening gesture in some species (de Waal 2003; Fuentes and Gamerl 2005).

Increased aggression as a result of increased visitor presence has been seen across primate species: mandrills and mangabeys showed increased aggression following increased visitor numbers (Chamove et al. 1988; Mitchell et al. 1991); siamangs and orangutans displayed more aggressive behaviour when threatening gestures (e.g. yawning) were performed by visitors (Nimon and Dalziel 1992; Birke 2002). Conversely, aggression in capuchins was reduced when direct visual contact with visitors was hindered (Sherwen et al. 2015).

This study examines the effect of visitor number and noise levels upon the behaviour of three ape species: western lowland gorillas *Gorilla gorilla gorilla*, Bornean orangutans *Pongo pygmaeus*, and pileated gibbons *Hylobates pileatus.* The inclusion of three species allows for comparisons of reactions across the family Hominoidea. The aim of the study was to establish whether visitors affected the ape groups, and how this potential effect manifested in behavioural change.

Methods and materials

Animals and enclosures

The study subjects were six western lowland gorillas with an average age of 12.92 years ±10.60, five Bornean orangutans with an average age of 19.20 years ±9.18 and four pileated gibbons with an average age of 12.08 years ±13.19 (Table 1). All animals were housed at Blackpool Zoo, UK. The gorilla enclosure consisted of an indoor and outdoor area, between which constant access was provided except during cleaning. Access was given to 'Gorilla Mountain', an additional outdoor enclosure, on an ad-hoc basis. Orangutans and gibbons were housed in similar indoor-outdoor enclosures, with the orangutans housed in the same building as the gorillas and the gibbons in the 'Small Primate House'. All normal husbandry and feeding routines were observed for the duration of the study, with participants maintained on a typical diet. One gorilla and orangutan feed was provided during educational talks. Gorilla and gibbon groups were well-established at the time of the study; the zoo had received one orangutan (Jingga) in October 2017. Enclosures had remained unchanged for several years, with the most recent enclosure upgrade completed in 2014.

Data collection procedure

Data were collected twice per week, one species per session. Observations took place between 1000 and 1500, April-August 2018. Data for each species were collected on a rotating schedule, with three sessions of 10 min per individual daily. Prior to each session a 10-min habituation period was observed to allow participants to acclimatise to the researcher's presence (Mitchell et al. 1992b). Instantaneous sampling was used every 2 min to record the focal animal's behaviour (Table 2), the number of visitors present, the noise level (using a Precision Gold N05CC decibel meter), and any additional information, for example, participants in a social interaction. A sampling interval of 2 min was

Table 2. An ethogram of all behaviours observed across the three species. Species-specific behaviours are denoted by ^{1}(gorilla), ^{2}(orangutan) and ^{3}(gibbon). Adapted from Braendle & Geissman (1997), Cheyne (2006), Kuhar (2008), Collins & Marples (2016).

Behaviour	Description
Aggression (conspecific)	Biting, hitting, chasing (non-play) threatening to bite^3, charging^{1,2}, chest-beating^1
Feed	Looking for/handling food, eating, drinking
Grooming	Scratching, picking, licking
Inactive	Sitting, lying down, sleeping
Affiliative	Non-aggressive conspecific interactions; play, allogrooming, touching
Baby interaction	Playing with baby^{1,3}, feeding baby^{1,3}
Locomotion	Walking, non-chasing running, climbing, brachiating^3
Play	Playing with objects, rolling^2
Visitor attention	Staring
Stereotypy	Abnormal behaviours; hair-plucking^{1,2}, hands over ears^1, coprophagy^{1,2}, urophagia^{1,2}, regurgitate & re-ingest^2, repetitive swinging^3, self-harm^3
Other	Engaging in any behaviour other than those listed above
Back to window	Sitting with back to window or viewing area
Out of sight	Unable to see

selected to allow for a count of visitor numbers, recording of the noise level, and following of the focal animal between enclosures where necessary. Sampling order of individuals was determined by assigning each animal a number and using a random number generator before each sampling session. This resulted in a total of 180 observations per individual and a total of 1080 observations for gorillas, 900 for orangutans and 720 for gibbons.

Talks took place once daily for orangutans throughout the duration of the study, and once daily for gorillas from the start of the peak season (June). Additional talks took place throughout the day at neighbouring enclosures and affected the noise levels around the ape enclosures, therefore such talks were noted when they occurred. Data were collected during talks and analysed separately. Noise specific to visitors – inclusive of talks – was recorded, while other environmental sounds, for example, vans driving past enclosures, were excluded from analysis.

Statistical analysis

One orangutan (Summer) was removed from the dataset prior to analysis due to a veterinary procedure and her subsequent removal from the orangutan group interrupting data collection, resulting in 720 observations for orangutans, which were split into 'before' and 'after'. All tests performed on orangutan data were performed on the 'before', 'after' and full datasets. Data were analysed using RStudio version 1.1. Tests were performed on complete datasets and with outliers removed: outliers were considered important as they consisted of visitor groups relevant to the zoo setting, such as school groups; removal of outliers allowed for comparison of results of data with and without these outlying social groups. A Shapiro-Wilk test was applied to visitor number and noise data to test for normality, after which the correlation coefficient was calculated for visitor number and noise and a linear regression model built to test whether visitor number was a significant predictor of noise levels. A Kruskal-Wallis test with post-hoc Wilcoxon was applied to test for differences in visitor number and noise levels between species. Wilcoxon tests were then applied to investigate differences in visitor number and noise during talks and feeds. Gibbons were excluded from this analysis as there were no scheduled talks or feeds for this species. Kruskal-Wallis tests were performed on complete gorilla and orangutan datasets and when split into 'during talk' and 'no talk', to establish whether talks had a significant effect on behaviour. Analysis of back to window behaviour was performed to test for a relationship with visitor number and noise using a generalised linear model (GLM). A GLM was also applied to the orangutan-specific behaviour of covering the head with a sack or bedding, to examine relationships with visitor number and noise. Visitor attention behaviour was tested to investigate the potential link between human-directed vigilance behaviours and increased visitor number and noise. On a species level, logistic regression was used to examine the effect of visitor number and noise on select behaviours (inactivity, locomotion and feeding). For all logistic regression tests, visitor number and noise were treated as continuous variables. A Kruskal-Wallis test was performed to investigate species differences in inactivity and locomotion, and a Pearson's Chi-squared test applied to examine whether feeding behaviour showed significant association with scheduled feeds. Locomotory behaviour was investigated alongside inactive behaviour as decreased inactivity may not necessarily lead to increased locomotion but, for example, aggression or vigilance. Stereotyping was observed in four gorillas but only one orangutan, therefore logistic regression was applied to the gorilla dataset and descriptive analysis performed for the orangutan data. Similarly, only two infants were observed in the study, so clinging behaviour was analysed descriptively. Analysis of Makari's clinging behaviour used the location 'inside' only, as when outside or on Gorilla Mountain his mother prevented him from walking; this was also applied during analysis of overall behaviour patterns. A Pearson's Chi-squared test was applied to the complete dataset by species, to examine differences in the behaviour patterns across visitor number and noise levels. For this analysis, visitor number and noise were grouped into three categories: 'low' (visitor number: ≤20, noise: ≤55.40 dB), 'medium' (visitor number: 21≤40, noise: 55.41≤79.90 dB) and 'high' (visitor number: ≥41, noise: ≥79.91 dB).

Results

Visitor number and noise

Visitor number and noise levels showed significant positive correlation (Figure 1), and a linear regression model showed that visitor number was a significant linear predictor of noise levels (Table 3). The species received different visitor numbers: gorillas received a mean of 8.6 and a maximum of 50, orangutans a mean of 9.5 and a maximum of 60, and gibbons a mean of 3.6 and a maximum of 30. There were significant differences in visitor numbers between gibbons and both gorillas and orangutans, but no significant difference between gorillas and orangutans. Noise levels between all three enclosures were significantly different (Table 3, Figure 2).

A significant relationship was seen between talks and visitor number (Figure 3); conversely there was no significant relationship between talks and noise (Figure 4, Table 4). There was no significant relationship between scheduled feeds and visitor number or noise (Table 4). Kruskal-Wallis tests found that talks had a significant relationship with behaviour in gorillas (X^2=24.524, df=11, P=0.01069) but not in orangutans (X^2=9.1594, df=9, P=0.4227).

Visitor avoidance and attention

Time spent with back to the window (BW) was not significantly influenced by visitor number or noise level (Table 5). When orangutan data were categorised as 'before' and 'after', analysis of data for BW showed no significant relationship with visitor number or noise levels in the 'before' dataset; after Summer's removal, a significant relationship was seen between BW and noise levels (Table 5). Application of the GLM showed a significant negative relationship between visitor number and orangutans covering their heads in the 'before dataset', inclusive of outliers, but this was not observed in the 'after' dataset or with noise levels (Table 5).

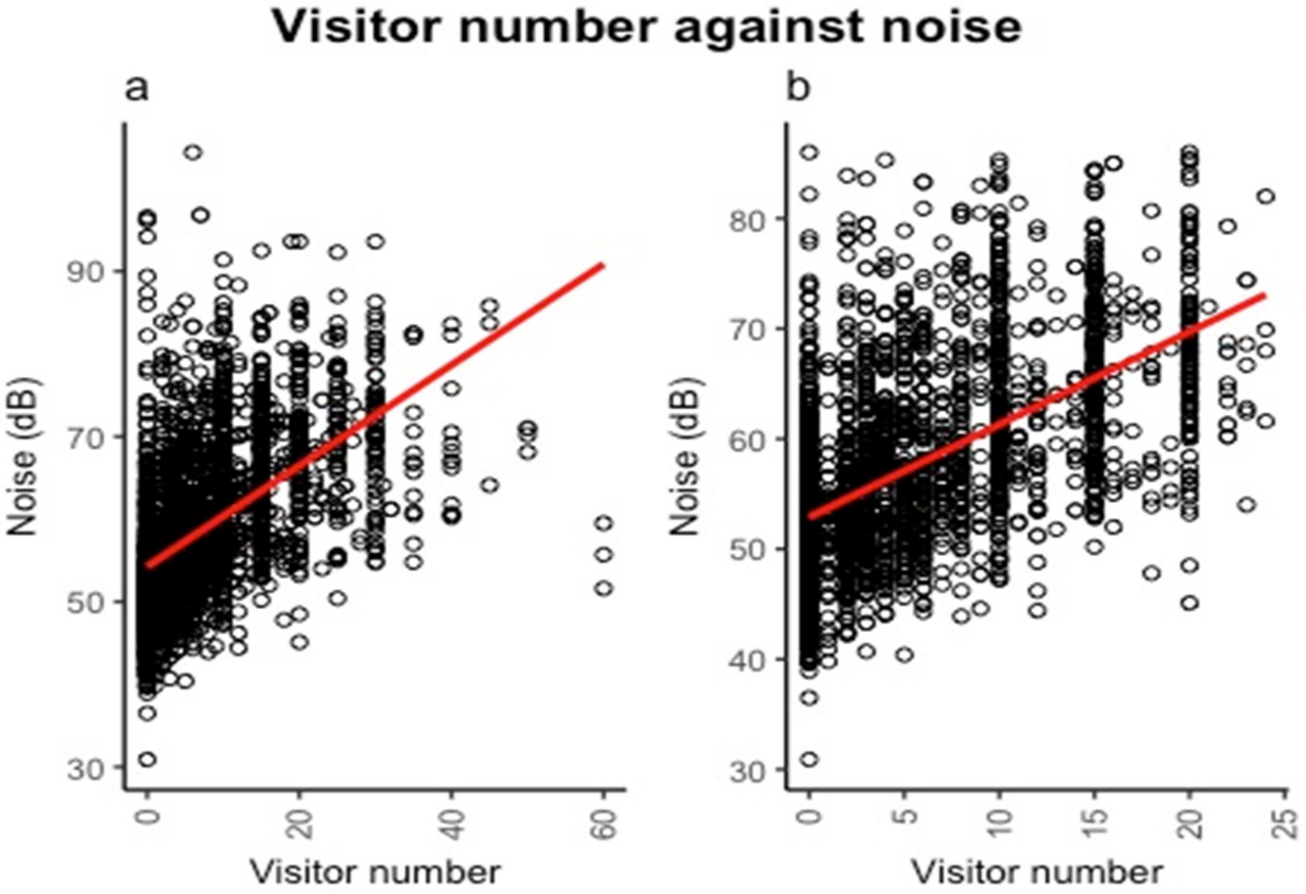

Figure 1. The relationship between visitor number and noise levels: A. Dataset containing outliers (r=0.53, t=31.48, df=2517, P<0.001); B. Dataset with outliers removed (r=0.54, t=32.088, df=2329, P<0.001).

Table 3. Test results for visitor number and noise. Significance levels are denoted by *(P<0.05) and ***(P<0.001).

Test	With outliers	Without outliers
Correlation (visitor number and noise)	r=0.5307664, t=31.479, df=2517, P<0.001***	r=0.5336781, t=32.088, df=2329, P<0.001***
Linear regression (visitor number and noise)	r^2=0.2814, f=987.2, df=2517, P<0.001***	r^2=0.3063, f=1030, df=2329, P<0.001***
Kruskal-Wallis (visitor numbers)	X^2=283.46, df=2, gorilla & orangutan P=0.09, gibbon & others P<0.001***	X^2 =216.93, df=2, gorilla & orangutan P=0.68, gibbon & others P<0.001***
Kruskal-Wallis (noise levels)	X^2=168.69, df=2, gorilla & orangutan P=0.02*, gibbon & others P<0.001***	X^2 =182.27 df=2, gorilla & orangutan P=0.013*, gibbon & others P<0.001***

Activity

Inactivity showed a significant negative relationship with visitor number in gorillas when outliers were included; analysis of orangutan and gibbon inactivity showed no significant relationships with visitor number or noise (Table 6). Analysis of locomotion showed no significant relationship with either factor in any species (P<0.005), and no significant differences in inactivity or locomotion were observed between species.

Feeding behaviour

In gorillas there was a significant positive relationship between feeding behaviour and visitor number, and a significant negative relationship between feeding and noise levels with outliers removed (Table 7). In orangutans, there was a significant positive relationship between feeding behaviour in the 'before' dataset with outliers, and the 'after' dataset (Table 7). Pearson's Chi-squared test showed no significant association between schedules feeds and feeding behaviour (P>0.05).

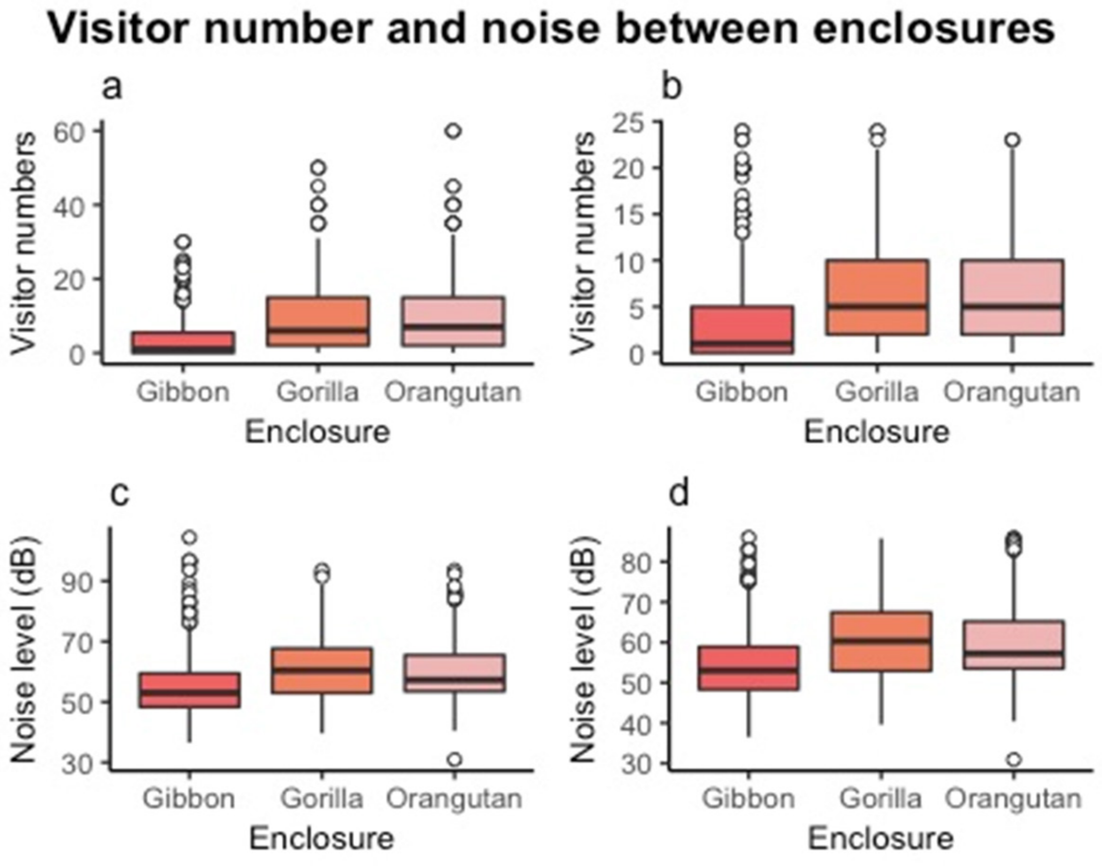

Figure 2. Differences in visitor numbers and noise levels between enclosures across the duration of the study (n=2520): A. Visitor number dataset containing outliers (X^2=283.46, df=2, gibbon and gorilla P<0.001, gibbon and orangutan P<0.001, gorilla and orangutan P=0.09); B. Visitor number dataset with outliers removed (X^2=215.93, df=2, gibbon and gorilla P<0.001, gibbon and orangutan P<0.001, gorilla and orangutan P=0.68); C. Noise dataset containing outliers (X^2=168.69, df=2, gibbon and gorilla P<0.001, gibbon and orangutan P<0.001, gorilla and orangutan P=0.02); D. Noise dataset with outliers removed (X^2=182.27, df=2, gibbon and gorilla P<0.001, gibbon and orangutan P<0.001, gorilla and orangutan P=0.013).

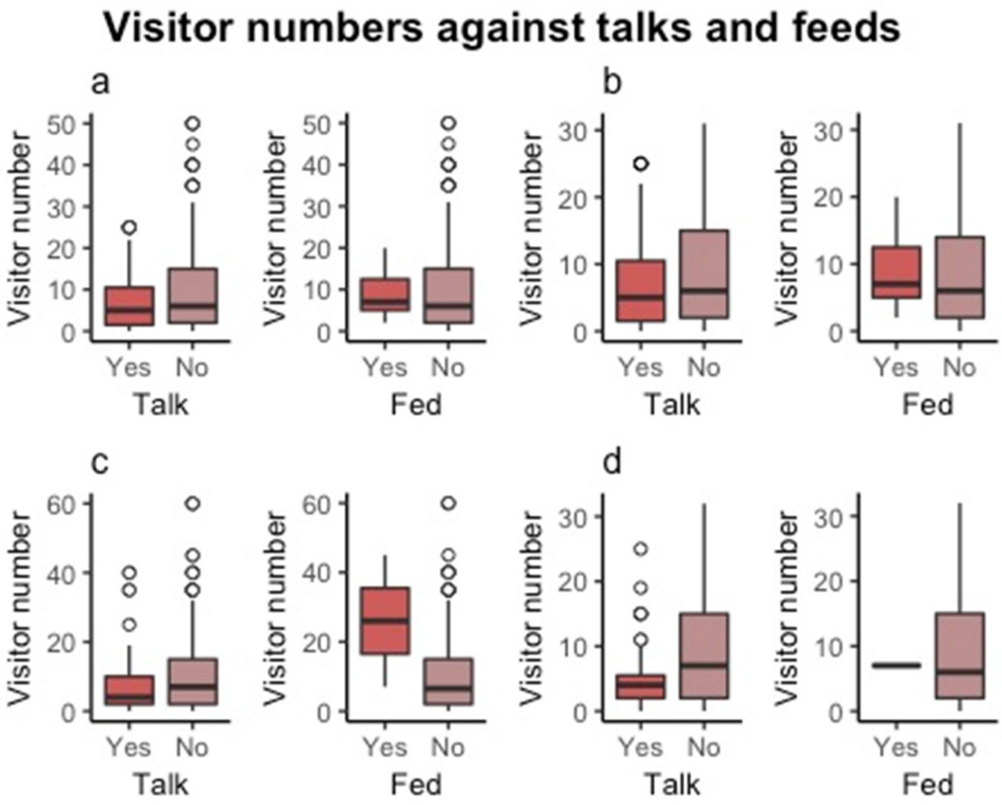

Figure 3. Differences in visitor number by enclosure when scheduled talks and feeds were taking place: A. Visitor number dataset for gorillas containing outliers; B. Visitor number dataset for gorillas with outliers removed; C. Visitor number dataset for orangutans containing outliers; D. Visitor number dataset for orangutans with outliers removed.

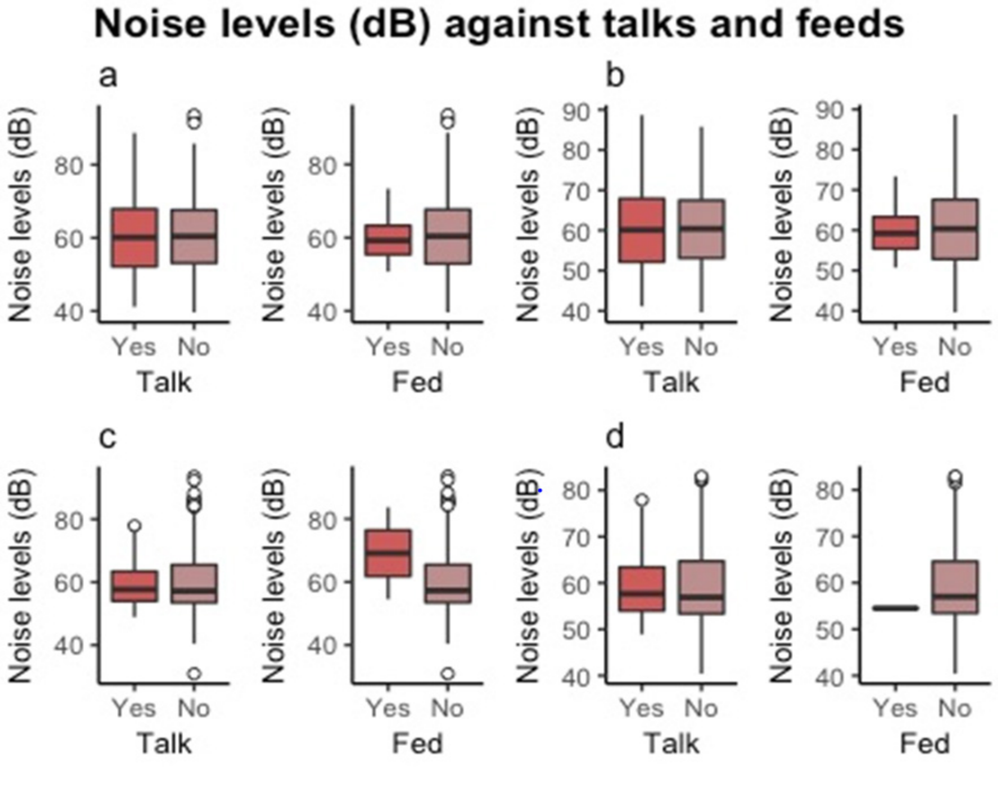

Figure 4. Differences in noise level by enclosure when scheduled talks and feeds were taking place: A. Noise dataset for gorillas containing outliers; B. Noise dataset for gorillas with outliers removed; C. Noise dataset for orangutans containing outliers; D. Noise dataset for orangutans with outliers removed.

Table 4. Test results for visitor number and noise in association with talks and feeds. Significance levels are denoted by *(P<0.05), **(P<0.01) and ***(P<0.001).

Test	With outliers	Without outliers
Wilcoxon (visitor number and talks)	W=210690, P=0.0002903***	W=202980, P=0.0002856***
Wilcoxon (visitor number and talks: gorillas)	W=90448, P=0.009673**	W=70831, P=0.02757*
Wilcoxon (visitor number and talks: orangutans)	W=22052, P=0.02011*	W=12514, P=0.001828**
Wilcoxon (noise and talks)	W=181700, P=0.769	W=180300, P=0.7875
Wilcoxon (noise and talks: gorillas)	W=80710, P=0.9852	W=80174, P=0.9587
Wilcoxon (noise and talks: orangutans)	W=18009, P=0.6967	W=17169, P=0.5045
Wilcoxon (visitor number and feeds)	W=12904, P=0.289	W=12320, P=0.4118
Wilcoxon (visitor number and feeds: gorillas)	W=7029.5, P=0.4222	W=8945.5, P=0.3515
Wilcoxon (visitor number and feeds: orangutans)	W=351, P=0.2102	W=370.5, P=0.9209
Wilcoxon (noise and feeds)	W=13969, P=0.5782	W=13850, P=0.5602
Wilcoxon (noise and feeds: gorillas)	W=8050.5, P=0.9584	W=8050.5, P=0.9434
Wilcoxon (noise and feeds: orangutans)	W=928, P=0.4757	W=223, P=0.5288

Table 5. Test results for visitor avoidance and attention behaviours (BW, hidden under sacks or bedding/IH and visitor attention/V). 'Before' and 'after' refer to the datasets before Summer's removal from the orangutan group and after her removal. Significance levels are denoted by *(P<0.05), **(P<0.01) and ***(P<0.001).

Test	With outliers	Without outliers
GLM (visitor number: gorillas BW)	z=0.843, P=0.3994	z=1.128, P=0.259
GLM (noise: gorillas BW)	z=-0.792, P=0.4282	z=-1.316, P=0.188
GLM (visitor number: orangutans BW)	z=0.003, P=0.998	z=0.329, P=0.742
GLM (noise: orangutans BW)	z=-1.503, P=0.133	z=-1.569, P=0.117
GLM (visitor number: orangutans 'before' BW)	z=-0.737, P=0.4612	z=0.02139, P=0.268
GLM (noise: orangutans 'before' BW)	z=-0.030, P=0.9763	z=-0.431, P=0.667
GLM (visitor number: orangutans 'after' BW)	z=0.564, P=0.5730	z=-0.007, P=0.9941
GLM (noise: orangutans 'after' BW)	z=-2.632, P=0.0085*	z=-2.391, P=0.0168*
GLM (visitor number: gibbons)	z=-1.347, P=0.1780	z=-2.451, P=0.0142
GLM (noise: gibbons)	z=-0.422, P=0.6732	z=0.629, P=0.5297
GLM (visitor number: orangutans IH)	z=-1.586, P=0.113	z=-2.054, P=0.040*
GLM (noise: orangutans IH)	z=-1.324, P=0.186	z=-0.523, P=0.601
GLM (visitor number: orangutans 'before' IH)	z=-2.131, P=0.0331*	z=-1.326, P=0.185
GLM (noise: orangutans 'before' IH)	z=-0.657, P=0.5110	z=-0.347, P=0.729
GLM (visitor number: orangutans 'after' IH	z=1.101, P=0.271	z=0.422, P=0.673
GLM (noise: orangutans 'after' IH)	z=-1.436, P=0.151	z=-1.117, P=0.264
GLM (visitor number: gorillas V)	z=1.253, P=0.210	z=1.438, P=0.151
GLM (noise: gorillas V)	z=-1.415, P=0.157	z=-1.520, P=0.128
GLM (visitor number: orangutans V)	z=-0.006, P=0.9950	z=0.636, P=0.5247
GLM (noise: orangutans V)	z=2.347, P=0.0189*	z=2.046, P=0.0408*
GLM (visitor number: orangutans 'before' V)	z=0.465, P=0.6418	z=1.051, P=0.2930
GLM (noise: orangutans 'before' V)	z=2.495, P=0.0126*	z=1.778, P=0.0755
GLM (visitor number: orangutans 'after' V)	z=0.076, P=0.939	z=-0.144, P=0.886
GLM (noise: orangutans 'after' V)	z=-0.202, P=0.840	z=-0.138, P=0.890
GLM (visitor number: gibbons V)	z=3.063, P=0.00219**	z=4.293, P<0.001***
GLM (noise: gibbons V)	z=0.678, P=0.49777	z=1.328, P=0.184

Table 6. Test results for inactivity. Significance levels are denoted by **(P<0.01).

Test	With outliers	Without outliers
GLM (visitor number: gorillas)	z=-2.749, P=0.00597**	z=-1.572, P=0.116
GLM (noise: gorillas)	z=0.688, P=0.49167	z=0.299, 0.765
GLM (visitor number: orangutans)	z=-1.797, P=0.0724	z=-1.142, P=0.254
GLM (noise: orangutans)	z=-0.027, P=0.9783	z=-0.166, P=0.868
GLM (visitor number: orangutans 'before')	z=-1.564, P=0.118	z=-0.951, P=0.341
GLM (noise: orangutans 'before')	z=-0.530, P=0.596	z=-0.675, P=0.499
GLM (visitor number: orangutans 'after')	z=-0.984, P=0.325	z=-0.804, P=0.421
GLM (noise: orangutans 'after')	z=1.050, P=0.294	z=1.361, P=0.174
GLM (visitor number: gibbons)	z=-0.628, P=0.530	z=-1.211, P=0.226
GLM (noise: gibbons)	z=-1.447, P=0.148	z=-0.111, P=0.912

Stereotypic behaviour

Four gorillas and one orangutan showed stereotypic behaviour. In gorillas, visitor number and noise showed no significant relationship with stereotyping (P>0.05). Stereotyping in the orangutan did not appear to be consistent with higher visitor numbers or noise levels.

Clinging behaviour

Incidence of clinging behaviour was examined with regards to visitor number and noise. There was a roughly even distribution of clinging behaviour across visitor number and noise levels in both infants.

Changes in behaviour during talks

Datasets were split into 'during talk' and 'no talk' and tested by species: behaviours tested were BW, hiding under bedding or sacks, visitor attention, inactivity, locomotion and feeding (Table 8).

There was no significant association between active or inactive behaviour and visitor number or noise in gorillas, and the complete and 'after' orangutan datasets; the 'before' dataset showed a significant relationship between active and inactive behaviours and noise (Table 9). Gibbon data showed a significant relationship between active behaviour and noise (Table 10).

Discussion

The visitor effect on zoo-housed primates ranged from no effect to detrimental as in previous literature (no effect: Mather 1999; Collins et al. 2017; increased stress: Mitchell et al. 1992b; Wormell et al. 1996; Birke 2002; Davis et al. 2005; Collins and Marples 2016). In this study, visitor number and noise had significant but contrasting relationships with several behaviours; the extent differed on a species level, as seen previously (Quadros et al. 2014). Furthermore, there were marked differences in the number of visitors at each enclosure in this study. Location may explain this

Table 7. Test results for feeding behaviour. Significance levels are denoted by *(P<0.05), **(P<0.01) and ***(P<0.001).

Test	With outliers	Without outliers
GLM (visitor number: gorillas)	z=3.135, P=0.00172**	z=3.389, P=0.000701***
GLM (noise: gorillas)	z=-2.406, P=0.01615	z=-2.574, P=0.010057*
GLM (visitor number: orangutans)	z=2.892, P=0.00383**	z=2.999, P=0.00271**
GLM (noise: orangutans)	z=-0.061, P=0.95148	z=-0.931, P=0.35211
GLM (visitor number: orangutans 'before')	z=2.156, P=0.03110*	z=1.750, P=0.0802
GLM (noise: orangutans 'before')	z=0.144, P=0.88539	z=0.015, P=0.9882
GLM (visitor number: orangutans 'after')	z=2.150, P=0.0316*	z=2.840, P=0.00451**
GLM (noise: orangutans 'after')	z=-0.440, P=0.6603	z=-1.202, P=0.22949

Table 8. Back to window (BW), visitor attention (V), inactivity (I), locomotion (L) and feeding (F) behaviours were tested after the dataset was split by when talks were taking place ('during') and when talks were not ongoing ('no talk'). Significance levels are denoted by *(P<0.05), **(P<0.01) and ***(P<0.001). This table includes significant results only; for full results, see Supplementary Materials.

Test	With outliers	Without outliers
Noise: orangutans 'after'; BW; no talk	z=-2.536, P=0.0112*	z=-2.165, P=0.0304*
Noise: orangutans; V; no talk	z=2.129, P=0.0333*	z=1.807, P=0.0708
Noise: orangutans 'before'; V; no talk	z=2.323, P=0.0202*	z=1.385, P=0.165950
Visitor number: gorillas; I; no talk	z=-3.318, P=0.000905***	z=-2.105, P=0.0354*
Visitor number: gorillas; L; no talk	z=2.461, P=0.0.0139*	z=0.650, P=0.5255
Noise: gorillas; L; no talk	z=-2.300, P=0.0215*	z=-2.111, P=0.0348*
Visitor number: gorillas; F; no talk	z=3.277, P=0.00105**	z=3.559, P=0.000372***
Noise: gorillas; F; no talk	z=-2.671, P=0.00757**	z=-2.890, P=0.003848**
Visitor number: orangutans; F; during	z=2.331, P=0.0197*	z=-0.003, P=0.998
Visitor number: orangutans; F; no talk	z=0.2.269, P=0.02325*	z=2.721, P=0.0065**
Visitor number: orangutans 'after'; F; no talk	z=1.417, P=0.157	z=2.445, P=0.0145*

difference: the gorilla and orangutan enclosures neighbour each other in a busy area of the zoo. The gibbon enclosure is in a lesser-visited location, so the species draws fewer visitors. Talks are held daily for the orangutans and, during the summer, the gorillas. This is not the case for gibbons; therefore, less attention is actively drawn to the species.

Animals sitting with their back to the window is a visitor avoidance behaviour and has been denoted a stress indicator (Collins and Marples 2016). In this study, all individuals sat with their back to the window. However, there was no significant relationship between physical orientation and visitor number and noise in gorillas and gibbons. A significant relationship between BW behaviour and noise levels was seen in orangutans after Summer's removal. Contrary to Birke (2002), the orangutans in this study decreased their use of sacks or bedding as cover when visitor number and noise levels increased. The hypothesis that an increased visitor number or noise level would lead to increased visitor attention behaviour (from here referred to as vigilance) as opposed to avoidance behaviours was tested alongside BW behaviour and use of sacks and bedding in orangutans. Vigilance showed no significant relationship with increased visitor number; however, as noise increased, vigilance behaviour increased. This suggests that, alongside the decrease in BW behaviour, vigilance is promoted above visitor avoidance behaviours in this orangutan group.

Table 9. Active and inactive behavioural categories were created prior to analysis. Species-specific behaviours are denoted by *(gorilla and gibbon) and **(orangutan).

Active	Inactive
Aggression (conspecific) 'AC'	Inactive 'I'
Affiliative 'AF'	Inactive hidden 'IH'**
Affiliative with mother 'AFM'*	Visitor attention 'V'
Attention to baby 'B'*	
Feeding 'F'	
Grooming 'G'	
Locomotion 'L'	
Other 'O'	
Play 'P'	
Stereotyping 'S'	

As visitor numbers increased, inactivity decreased. Again, species differences were evident: gorilla inactivity levels declined significantly with increasing visitor number but showed no significant relationship with noise. Orangutan and gibbon inactivity levels were unaffected by visitor number and noise. This suggests visitor number alone affected inactivity. Furthermore, there was no significant effect of visitor number or noise level on locomotory behaviour. Decreased inactivity with increased crowd size has been repeatedly observed in primates (Hosey and Druck 1987; Chamove et al. 1988; Mitchell et al. 1992a; Wells 2005) and a change in inactivity may be used as a baseline for investigating other behaviours that may be performed instead. An increase in locomotion does not necessarily follow declined inactivity levels, but instead increased aggression or vigilance behaviour, for example. Species differences have been suggested to mitigate potential effects of visitors; for example, gibbons are more active than gorillas (Collins and Marples 2016), and this will impact on inactivity – and reactions to visitor presence and behaviour – in both species. However, in this study, there was no significant difference in overall levels of inactivity and locomotion between species.

Excitation was not tested directly in this study, rather through the testing of visitor number and noise with inactivity and locomotion; however, whether this impacts on welfare is dependent on baseline activity levels. These may be difficult to ascertain: establishing accurately at what noise level background noise may begin to cause health, welfare or behavioural problems is problematic, especially within a zoological institution which would only allow for data collection of background noise before and after closing. Furthermore, the strength of causation on each side is unknown: if visitor number, noise levels and animal activity are bidirectional (Margulis et al. 2003), is increased activity due to increased visitor numbers and/or noise, or are visitor numbers and/or noise increasing due to increased activity? Previous research has shown that zoo visitors are more attracted to more active animals (Bitgood et al. 1988; Altman 1999; Margulis et al. 2003; Moss and Esson 2010). Wild animal activity budgets may

Table 10. The results from the Pearson's Chi-squared tests for all datasets. Active and inactive datasets are as those defined in Table 9. Not all behaviours in each dataset were present for each species: aside from the species-specific behaviours denoted in Table 9, conspecific-directed aggression was not recorded for orangutans. Significance levels are denoted by *(P<0.05) and **(P<0.01).

Test	Results
Gorilla active behaviour and visitor number	X^2=19.831, df=18, P=0.3424
Gorilla active behaviour and noise	X^2=20.546, df=18, P=0.3029
Gorilla inactive behaviour and visitor number	X^2=0.32906, df=2, P=0.8483
Gorilla inactive behaviour and noise	X^2=0.36069, df=2, P=0.835
Orangutans active behaviour and visitor number	X^2=12.568, df=12, P=0.4012
Orangutans active behaviour and noise	X^2=17.483, df=12, P=0.1323
Orangutans inactive behaviour and visitor number	X^2=1.7163, df=4, P=0.7877
Orangutans inactive behaviour and noise	X^2=6.1232, df=4, P=0.1901
Orangutans 'before' active behaviour and visitor number	X^2=19.002, df=12, P=0.08848
Orangutans 'before' active behaviour and noise	X^2=23.102, df=12, P=0.02687*
Orangutans 'before' inactive behaviour and visitor number	X^2=1.105, df=2, P=0.05755
Orangutans 'before' inactive behaviour and noise	X^2=10.506, df=4, P=0.03272*
Orangutans 'after' active behaviour and visitor number	X^2=9.3801, df=12, P=0.6702
Orangutans 'after' active behaviour and noise	X^2=12.113, df=12, P=0.4367
Orangutans 'after' inactive behaviour and visitor number	X^2=0.62488, df=4, P=0.9603
Orangutans 'after' inactive behaviour and noise	X^2=1.3477, df=4, P=0.8532
Gibbons active behaviour and visitor number	X^2=2.363, df=9, P=0.9843
Gibbons active behaviour and noise	X^2=36.16, df=18, P=0.00673**
Gibbons inactive behaviour and visitor number	X^2=0.32906, df=1, P=0.8943
Gibbons inactive behaviour and noise	X^2=1.0341, df=2, P=0.5963

be used for comparison where available, but this comes with its own difficulties and may lead to inaccurate comparisons (Veasey et al. 1996; Howell and Cheyne 2019). It is difficult to say whether decreased inactivity alongside rising visitor numbers and/or noise levels indicates decreased welfare, especially if decreased inactivity is accompanied by a rise in benign activities (e.g. affiliative behaviours) rather than the increased aggression observed in some studies (Chamove et al. 1988; Mitchell et al. 1991; Fa 1992; Mitchell et al. 1992a; Wells 2005; Kuhar 2008; Stoinski et al. 2012; Collins and Marples 2016). As stated by Birke (2002) it is difficult to judge the effect of increased activity levels, even in species where we hold baseline data. However, if increased locomotion is expressed in stereotypic pacing, this cannot be considered a desirable outcome. Previous studies have indicated the importance of off-show areas for primates (e.g. Kuhar 2008) to avoid decreased inactivity and related increases in negative behaviours, suggesting that increased visitor numbers may be a welfare concern in institutions whose enclosures do not contain freely accessible off-show areas.

There was a significant positive relationship between visitor number and feeding behaviour in gorillas and the complete and 'after' orangutan datasets. However, a significant, negative, relationship between noise and feeding behaviour was seen only in gorillas. Previous studies have shown that feeding decreased with increased visitor number (Chamove et al. 1988; Mitchell et al. 1991; Fa 1992; Wells 2005; Kuhar 2008; Collins and Marples 2016); however, it has also been suggested that feeding enrichment may help to reduce the visitor effect (Birke 2002; Carder and Semple 2008; Clark et al. 2011). Feeding enrichment includes scatter feeding, which was used at Blackpool Zoo. At least one feed daily was conducted during the gorilla and orangutan talks. There was a significant effect of talks on visitor number at both enclosures, suggesting that visitors are drawn to enclosures by talks (Mitchell et al. 1992a). Talks did not have a significant effect on noise levels and scheduled feeds had no significant effect on visitor numbers or noise levels. This is suggested to be because, although one feed was advertised in conjunction with the talk, the other daily feeds were not advertised and visitors may not be aware that they were taking place. Talks showed a significant relationship with behaviour in gorillas but there was no significant association between scheduled feeds and feeding behaviour. In this study, there is no evidence that feeds reduced the incidence of unwanted behaviours through increased feeding behaviour. However, the increase in feeding alongside increased visitor number may be explained by the visitor attention hypothesis. The reduction of feeding in gorillas with increased noise, however, highlights a potential detrimental effect of active visitors in this species.

A more indicative measure of behavioural change due to visitors is infants clinging to their mother. Clinging is a fear response and may be a more reliable indicator of the visitor effect; other indicators, such as aggression, may be caused by circumstances other than visitor presence or noise (e.g. food- or resource-related aggression). Increases in clinging may indicate that infants find visitor presence and/or noise stressful, perhaps due to perceived threat (Birke 2002; Kuhar 2008; Collins and Marples 2016). This was not seen in this study: clinging was not affected by visitor number or noise. Further research into this effect is required; the current study only examined two infants of different species, who were not monitored from birth. A linking hypothesis suggests that the birth of an infant may be enriching for other group members, reducing the visitor effect (Smith and Kuhar 2010; Collins and Marples 2016). These two topics may be studied concurrently to provide more data on the visitor effect on infants and adults post-birth. In this study, interactions were observed between infants

https://doi.org/10.19227/jzar.v8i4.523

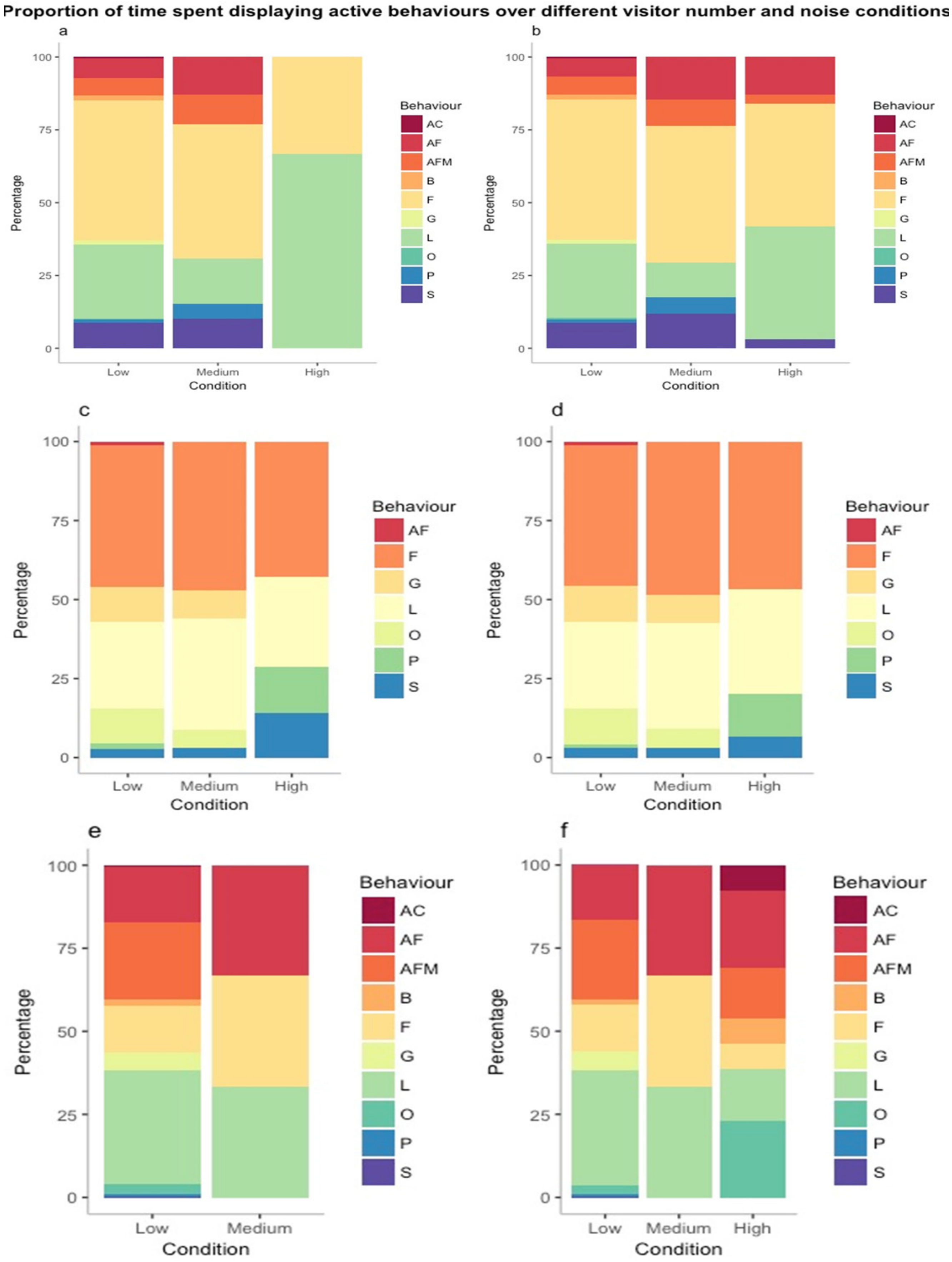

Figure 5. The graphs show the proportion of time each species displayed active behaviours: conspecific-directed aggression (AC), affiliative (AF), clinging (AFM), attention to the baby (B), feeding (F), grooming (G), locomotion (L), other (O), play (P) and stereotyping (S). 'Low', 'medium' and 'high' visitor number and noise conditions are as defined in Methods: A. Proportion of time gorillas spent performing active behaviours across different visitor conditions; B. Proportion of time gorillas spent performing active behaviours across different noise conditions; C. Proportion of time orangutans spent performing active behaviours across different visitor conditions; D. Proportion of time orangutans spent performing active behaviours across different noise conditions; E. Proportion of time gibbons spent performing active behaviours across different visitor conditions; F. Proportion of time gibbons spent performing active behaviours across different noise conditions.

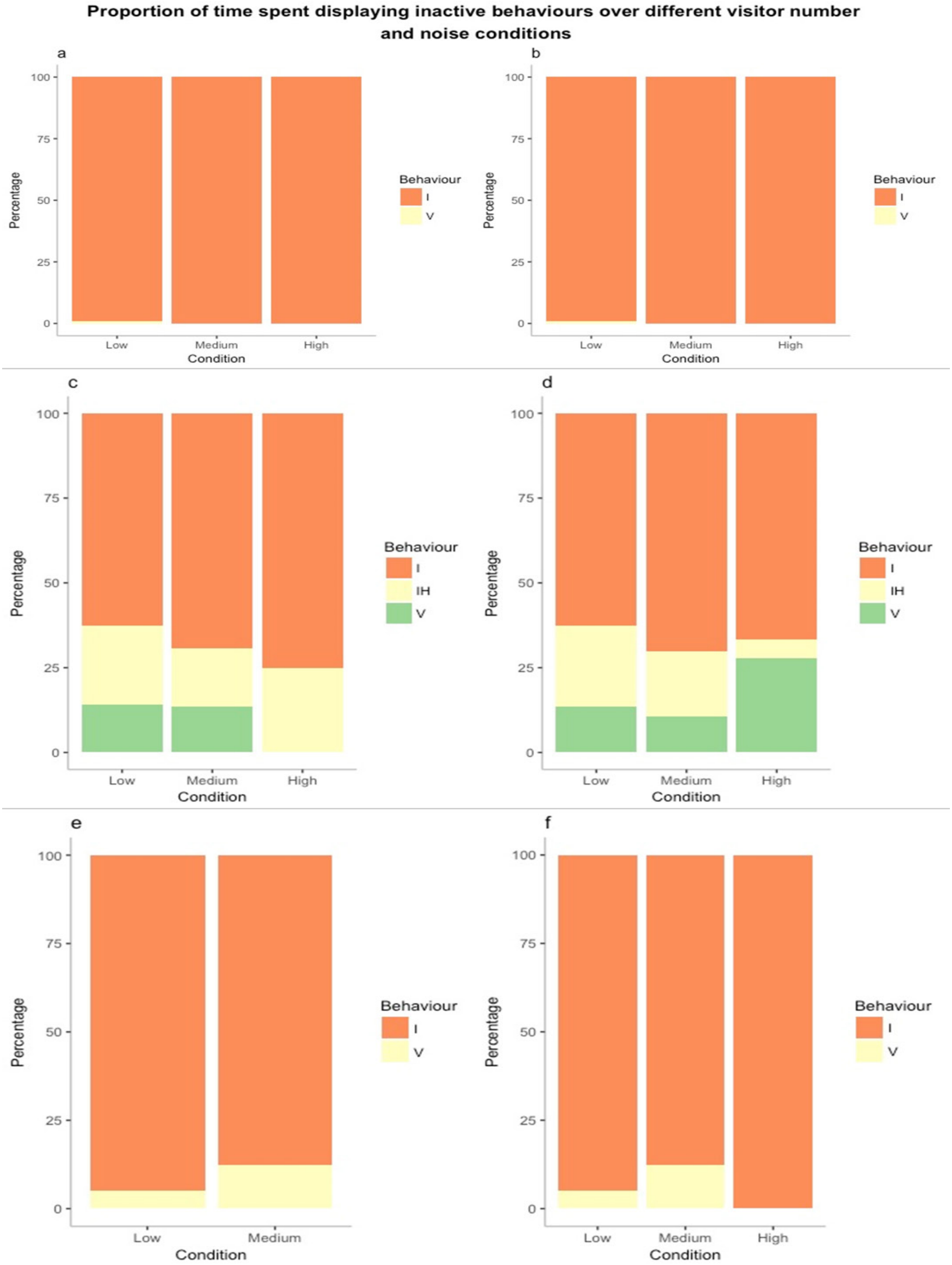

Figure 6. The graphs show the proportion of time each species spent displaying inactive behaviours: inactive (I), hidden under sacks or bedding (IH) and visitor attention (V). 'Low', 'medium' and 'high' visitor number and noise conditions are as defined in Methods: A. Proportion of time gorillas spent performing inactive behaviours across different visitor number conditions; B. Proportion of time gorillas spent performing inactive behaviours across different noise conditions; C. Proportion of time orangutans spent performing inactive behaviours across different visitor number conditions; D. Proportion of time orangutans spent performing inactive behaviours across different noise conditions; E. Proportion of time gibbons spent performing inactive behaviours across different visitor number conditions; F. Proportion of time gibbons spent performing inactive behaviours across different noise conditions.

and all group members. Whether this replicated the effect seen in Collins and Marples (2016) cannot be said due to the lack of data prior to the infants' birth. However, this may be useful to investigate further as the effect of birth on social groups is currently understudied (Collins and Marples 2016).

Stereotypic behaviour has been identified as a stress response in apes (Blaney and Wells 2004; Wells 2005; Carder and Semple 2008; Stonski et al. 2012; Collins and Marples 2016). There was differing prevalence of stereotyping across the species, with four gorillas and one orangutan showing stereotypies, whereas gibbons showed no stereotypy. Furthermore, stereotypies varied between species: gorillas most commonly performed coprophagy where the orangutan showed mostly regurgitation and reingestion. This illustrates different reactions to visitors and noise across individuals and species, which could come from a range of factors, for example, life history, personality and housing (Hosey 2000; Hosey 2005; Choo et al. 2011; Collins and Marples 2016; Sherwen and Hemsworth 2019), as well as differing levels of visitors between species. The results of this study align with those of Smith and Kuhar (2010), in which zoo-housed white-cheeked gibbons and siamangs showed no abnormal or unwanted behaviours. This may be because these animals had freely accessible off-show areas to 'escape' visitors (Smith and Kuhar 2010); that creating freely-accessible areas of privacy within enclosures reduces stress and the incidence of abnormal or unwanted behaviours has been seen in other primates and taxa, even if these areas are not used (Blaney and Wells 2004; Fernández et al. 2009; Bloomfield et al. 2015). In this study, freely accessible off-show areas were not provided; a potential effect of this is the increase in stereotyping in the orangutan individual and decreased inactivity in gorillas and orangutans with increased visitor number. However, that not all animals in the current study displayed stereotypies illustrates the complexity of factors controlling responses to visitor number and noise. Furthermore, the gorillas that did not show stereotypies were mother and offspring, suggesting the effect of a new infant may have been present.

However, the effects of factors such as life history, previous husbandry or environment, and personality should not be understated. Reactions to visitor number and noise varied greatly between species and individuals, with gibbons appearing most able to cope with captivity. Whether this is due to life history, being more habituated to human presence, or simply receiving fewer visitors cannot be discerned; however, this aligns with the findings of Smith and Kuhar (2010), who found that other *Hylobates* species showed few behavioural differences in response to visitors. Conversely, great apes have been repeatedly judged as negatively affected by visitor number and noise (e.g. Birke 2002; Blaney and Wells 2004; Carder and Semple 2008; Collins and Marples 2016). One explanation is the evolutionary proximity of humans to non-human primates, creating the propensity for actions displayed by human visitors (e.g. staring, yawning) to be interpreted as threatening by great apes (Birke 2002) and other primates such as siamangs and capuchins (Nimon and Dalziel 1992; Sherwen et al. 2015). However, the potential effects of species differences on reactions to visitors and noise in zoo settings have been understudied, as have those of personality (Sherwen and Hemsworth 2019). Both of these areas deserve attention, as a deeper understanding of species' and individuals' reactions to visitors may allow more targeted approaches to mitigate the effects of visitors and noise, for example, designing enclosures where visitors are 'below' animals for arboreal species (e.g. Chamove et al. 1988; Choo et al. 2011).

Regarding drivers of stress in captive primates, with the captive environment comes a lack of control, and adding off-show areas or equivalent, for example, privacy screens, to be used at will returns some control to animals, potentially reducing the incidence of unwanted behaviours. Visitor presence and noise are factors that animals cannot control, adding to or perhaps causing the stress associated with visitors. Lack of control is linked to anxiety and stress (Morgan and Tromborg 2007), with some suggesting that feeling in control is essential to animal well-being (O'Neill 1989; Friend 1991) and that lack of control may impact physiological measures of welfare, for example, faecal cortisol (Mineka and Kelly 1989). Providing animals with the ability to control their environment has been suggested as a method to ameliorate the effects of stress caused by visitors and/or noise (Hanson et al. 1976; Wemelsfelder 1993; Wiepkema and Koolhaas 1993; Sambrook and Buchanan-Smith 1997; Hosey 2005; Smith and Kuhar 2010; Collins and Marples 2016).

To add control to the environment, it is suggested animals be given free access to off-show areas; however, not all institutions currently have enclosures with open access to appropriate off-show facilities, and the cost of renovating enclosures to provide off-show areas is prohibitive for many collections. Alternative modifications to enclosure design may create the perception of reduced body size of visitors, such as raising viewing windows so that only a visitor's head is visible (Chamove et al. 1988); although, unless enclosures are due for or undergoing renovation, the cost of these modifications may again prove too expensive for many collections. Alternative low-cost solutions may prove effective in reducing stress: previous studies have trialled solutions such as the use of cargo nets over windows to reduce direct visual contact between animals and visitors (Blaney and Wells 2004), and privacy screens (Kuhar 2008; Smith and Kuhar 2010; Bloomfield et al. 2015) or foliage (Kuhar 2008) as visual barriers. In this study, the only area with foliage as a barrier was Gorilla Mountain; however, foliage did not obstruct visual contact around the entire perimeter of the enclosure and the gorilla group rarely had open access to this area. Furthermore, none of these solutions, bar creating off-show areas, have the ability to reduce noise levels around enclosures. This is important as, in this study, some behaviours were significantly influenced by noise only. For this reason, zoos must monitor the behaviour of their visitors as far as practicable. This may be achieved through the stationing of staff or volunteers in the vicinity of enclosures, as their presence alone may help to reduce incidents of disruptive behaviour. This is seen at many walkthrough exhibits, although it is prohibitive in terms of cost and staff time for many zoos.

Eye-level signage, aimed at modifying visitor behaviour in a positive, rather than negative, manner may prove effective in reducing noise levels and random noise events, for example, banging on the glass (Kratochvil and Schwammer 1997), which may in turn reduce stress in captive primates. Furthermore, the use of netting over viewing windows positively influenced the behaviour of animals and visitors, who spoke less and more quietly when the net was in place, with fewer recorded incidents of visitors banging on the glass (Blaney and Wells 2004). The results of the current study suggest the introduction of a freely accessible off-show area may benefit the apes, whether this is achieved through the creation of a dedicated off-show area of the employment of low-cost visual barriers.

Acknowledgements

The authors would like to thank the primate keeping staff and Research Department at Blackpool Zoo, as well as Dr. Hannah Mossman, Dr. Danny Norrey and Prof. Richard Preziosi at Manchester Metropolitan University. Further thanks go to the anonymous reviewer whose comments helped to improve this manuscript.
The authors declare no conflicts of interest.

References

Altman J.D. (1998) Animal activity and visitor learning at the zoo. *Anthrozoös* 11(1): 12-20. doi: 10.1080/08927936.1998.11425083.

Birke L. (2002) Effects of browse, human visitors and noise on the behaviour of captive orang utans. *Animal Welfare* 11(2): 189-201.

Bitgood S., Patterson D., Benefield A. (1988) Exhibit design and visitor behaviour: empirical relationships. *Environment and Behaviour* 20: 474-490. doi: 10.1177/0013916588204006.

Blaney E.C., Wells D.L. (2004) The influence of a camouflage net barrier on the behaviour, welfare and public perception of zoo-housed gorillas. *Animal Welfare* 13(2): 111-120.

Bloomfield R.C., Gillespie G.R., Kerswell K.J., Butler K.L., Hemsworth P.H. (2015) Effect of partial covering of the visitor viewing area window on positioning and orientation of zoo orangutans: a preference test. *Zoo Biology* 34(3): 223-229. doi: 10.1002/zoo.21207.

Bloomsmith M.A., Marr M.J., Maple T.L. (2007) Addressing nonhuman primate behavioral problems through the application of operant conditioning: is the human treatment approach a useful model? *Applied Animal Behaviour Science* 102(3-4): 205-222. doi: 10.1016/j.applanim.05.028.

Bortolini T.S., Bicca-Marques J.C. (2011) The effect of environmental enrichment and visitors on the behaviour and welfare of two captive hamadryas baboons (*Papio hamadryas*). *Animal Welfare* 20: 573-579.

Botreau R., Veissier I., Butterworth A., Bracke M.B.M.; Keeling L.J. (2007) Definition of criteria for overall assessment of animal welfare. *Animal Welfare* 16: 225-228.

Braendle C., Geissman T. (1997) Behavioural development of a pileated gibbon (*Hylobates pileatus*). *International Zoo News* 44(1): 4-16.

Carder G., Semple S. (2008) Visitor effects on anxiety in two captive groups of Western lowland gorillas. *Applied Animal Behaviour Science* 115(3-4): 211-220. doi: 10.1016/j.applanim.2008.06.001.

Chamove A.S., Hosey G.R., Schaetzel P. (1988) Visitors excite primates in zoos. *Zoo Biology* 7(4): 359-369. doi: 10.1002/zoo.1430070407.

Cheyne S. (2006) Unusual behaviour of captive-raised gibbons: implications for welfare. *Primates* 47(4): 322-326. doi: 10.1007/s10329-006-0190-z.

Choo Y., Todd P.A., Li D. (2011) Visitor effects on zoo orangutans in two novel, naturalistic enclosures. *Applied Animal Behaviour Science* 133(1): 78-85. doi: 10.1016/j.applanim.2011.05.007.

Clark F.E., Fitzpatrick M., Hartley A., King A.J., Lee T., Routh A., Walker S.L., George K. (2011) Relationship between behavior, adrenal activity, and environment in zoo-housed Western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biology* 31(3): 306-320. doi: 10.1002/zoo.20396.

Collins C.K., Marples N.M. (2016) The effects of zoo visitors on a group of Western lowland gorillas *Gorilla gorilla gorilla* before and after the birth of an infant at Dublin Zoo. *International Zoo Yearbook* 50(1): 183-193. doi: 10.1111/izy.12111.

Collins C., Corkery I., Haigh A., McKeown S., Quirke T., O'Riordan R. (2017) The effects of environmental and visitor variables on the behavior of free-ranging ring-tailed lemurs (*Lemur catta*) in captivity. *Zoo Biology* 36(4): 250-260. doi: 10.1002/zoo.21370.

Cooke C.M., Schillaci M.A. (2007) Behavioral responses to the zoo environment by white handed gibbons. *Applied Animal Behaviour Science* 106: 125-133. doi: 10.1016/j.applanim.2006.06.016.

Davis N., Schaffner C.M., Smith T.E. (2005) Evidence that zoo visitors influence HPA activity in spider monkeys (*Ateles geoffroyii rufiventris*). *Applied Animal Behaviour Science* 90(2): 131-141. doi: 10.1016/j.applanim.2004.08.020.

Fa J. (1989) 'Influence of people on the behaviour of display primates'. In Segal, E.F. (ed.) *Housing, care and psychological well-being of captive and laboratory primates.* Park Ridge, NJ: Noyes Publications, pp. 270-290.

Fa J.E. (1992) Visitor-directed aggression among the Gibraltar macaques. *Zoo Biology* 11(1): 43-52. doi: 10.1002/zoo.1430110106.

Fernández E.J., Tamborski M.A., Pickens S.R., Timberlake W. (2009) Animal-visitor interactions in the modern zoo: Conflicts and interventions. *Applied Animal Behaviour Science* 120(1-2): 1-8. doi: 10.1016/j.applanim.2009.06.002.

Friend T.H. (1991) Behavioral aspects of stress. *Journal of Dairy Science* 74(1): 292-303. doi: 10.3168/jds.S0022-0302(91)78173-3.

Hanson J.P., Larson M.E., Snowdon C.T. (1976) The effects of control over high intensity noise on plasma cortisol in rhesus monkeys. *Behavioral Biology* 16(3): 333-340. doi: 10.1016/S0091-6773(76)91460-7.

Hemsworth P.H., Sherwen S.L., Coleman G.J. (2018) 'Human contact.' In Appleby, M.C., Olsson, I.A.S. & Gilando, F. (eds.) *Animal Welfare*. 3rd ed., Wallingford, U.K.: CAB International, pp. 294-314.

Hosey G.R. (2000) Zoo animals and their human audiences: what is the visitor effect? *Animal Welfare* 9: 343-357.

Hosey G.R. (2005) How does the zoo environment affect the behaviour of captive primates? *Applied Animal Behaviour Science* 90(2): 107-129. doi: 10.1016/j.applanim.2004.08.015.

Hosey G. (2013) Hediger revisited: how do zoo animals see us? *Journal of Applied Animal Welfare Science* 16: 338-359. doi: 10.1080/10888705.2013.827916.

Hosey G.R., Druck P.L. (1987) The influence of zoo visitors on the behaviour of captive primates. *Applied Animal Behaviour Science* 18(1): 19-29. doi: 10.1016/0168-1591(87)90251-6.

Hosey G.R., Skyner L.J. (2007) Self-injurious behavior in zoo primates. *International Journal of Primatology* 28: 1431-1437. doi: 10.1007/s10764-007-9203-z.

Howell C.P., Cheyne S.M. (2019) Complexities of using wild versus captive activity budget comparisons for assessing captive primate welfare. *Journal of Applied Animal Welfare Science* 22(1): 78-96. doi: 10.1080/10888705.2018.1500286.

Kratochvil H., Schwammer H. (1997) Reducing acoustic disturbances by aquarium visitors. *Zoo Biology* 16(4): 349-353. doi: 10.1002/(SICI)1098-2361(1997)16:4<349::AID-ZOO7>3.0CO;2-A.

Kuhar C.W. (2008) Group differences in captive gorillas' reaction to large crowds. *Applied Animal Behaviour Science* 110(3-4): 377-385. doi: 10.1016/j.applanim.2007.04.011.

Margulis S.W., Hoyos C., Anderson M. (2003) Effect of felid activity on zoo visitor interest. *Zoo Biology* 22(6): 587-599. doi: 10.1002/zoo.10115.

Markovitz H., Stevens V., Mellon J., Barrow B. (1981) Performance of a mandrill (*Mandrillus sphinx*) in competition with zoo visitors and computer on a reaction-time game. *Acta Zoologica et Pathologica Antverpiensia* 76: 169-180.

Mather L. (1999) *Response of captive orang utans to a human audience*. MPhil, University of Manchester (Bolton Institute).

Mellor D.J., Patterson-Kane E., Stafford K.J. (2009) *The Sciences of Animal Welfare*. Oxford, U.K.: Wiley-Blackwell (UFAW Animal Welfare Series).

Mineka S., Kelly K.A. (1989) 'The relationship between anxiety, lack of control and loss of control'. In Steptoe, A. & Appels, E. (eds.) *Stress, personal control, and health*, Oxford, U.K.: Oxford University Press, pp. 163-191.

Mitchell G., Herring F., Obradovich S., Tromborg C., Dowd B., Neville L.E., Field L. (1991) Effects of visitors and cage changes on the behaviors of mangabeys. *Zoo Biology* 10(5): 417-423. doi: 10.1002/zoo.1430100505.

Mitchell G., Tromborg C.T., Kaufmann J., Bargabus S., Simoni R., Geissler V. (1992a) More on the 'influence' of zoo visitors on the behaviour of captive primates. *Applied Animal Behaviour Science* 35(2): 189-198. doi: 10.1016/0168-1591(92)90009-Z.

Mitchell G., Herring F., Tromborg C.T., Dowd B., Steiner S., Obradovich S. (1992b) Targets of aggressive facial displays by golden-bellied mangabeys (*Cercocebus galeritus chrysogaster*) at the Sacramento Zoo. *Applied Animal Behaviour Science* 33(2-3): 249-259. doi: 10.1016/s0168-1591(05)80012-7.

Moodie E., Chamove A. (1990) Brief threatening events beneficial for captive tamarins? *Zoo Biology* 9: 275-286.

Morgan K.N., Tromborg C.T. (2007) Sources of stress in captivity. *Applied Animal Behaviour Science* 102(3-4): 262-302. doi: 10.1016/j.applanim.2006.05.032.

Moss A., Esson M. (2010) Visitor interest in zoo animals and the implications for collection planning and zoo education programmes. *Zoo Biology* 29(6): 715-730. doi: 10.1002/zoo.20316.

Nimon A., Dalziel F. (1992) Cross-species interaction and communication: a study method applied to captive siamang (*Hylobates syndactylus*) and long-billed corella (*Cacatua tenuirostris*) contacts with humans. *Applied Animal Behaviour Science* 33: 261-272. doi: 10.1016/S0168-1591(05)80013-9.

O'Neill P. (1989) 'A room with a view for captive primates: issues, goals, related research and strategies'. In Segal, E.F. (ed.) *Housing, care, and psychological wellbeing of captive and laboratory primates.* Park Ridge, N.J., USA: Noyes Publications. pp. 135-160.

Owen M.A., Swaisgood R.R., Czekala N.M., Steinman K., Lindburg D.G. (2004) Monitoring stress in captive giant pandas (*Ailuropoda melanoleuca*): behavioral and hormonal responses to ambient noise. *Zoo Biology* 23: 147-164. doi: 10.1002/zoo.10124.

Ross S.R. (2006) Issues of choice and control in the behaviour of a pair of captive polar bears (*Ursus maritimus*). *Behavioural Processes* 73(1); 117-120. doi: 10.1016/j.beproc.2006.04.003.

Sambrook T.D., Buchanan-Smith H.M. (1997) Stereotypic animal behaviour. *Animal Welfare* 6: 207-216.

Sherwen S.L., Harvey T.J., Magrath M.J., Butler K.L., Fanson K.V., Hemsworth P.H. (2015) Effects of visual contact with zoo visitors on black-capped capuchin welfare. *Applied Animal Behaviour Science* 167: 65-73. doi: 10.1016/j.applanim.2015.03.004.

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

Smith K.N., Kuhar C.W. (2010) Siamangs (*Hylobates syndactylus*) and white-cheeked gibbons (*Hylobates leucogenys*) show few behavioral differences related to zoo attendance. *Journal of Applied Animal Welfare Science* 13(2): 153-163. doi: 10.1080/10888700903579895.

Stoinski T.S., Jaicks H.F., Drayton L.A. (2012) Visitor effects on the behavior of captive western lowland gorillas: the importance of individual differences in examining welfare. *Zoo Biology* 31(5): 586-598. doi: 10.1002/zoo.20425.

Veasey J.S., Waran N.K., Young R.J. (1996) On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator, using the giraffe (*Giraffa camelopardalis*) as a model. *Animal Welfare* 5(2): 139-153.

Wells D.L. (2005) A note on the influence of visitors on the behaviour and welfare of zoo-housed gorillas. *Applied Animal Behaviour Science* 93(1-2): 13-18. doi: 10.1016/j.applanim.2005.06.019.

Wemelsfelder F. (1993) 'The concept of animal boredom and its relationship to stereotyped behaviour'. In Rushenm A.B.L.a.J (ed.) *Stereotypic Animal Behaviour.* Wallingford, U.K.: Cab Intl, p. 31.

Wielebnowski N. (1998) 'Contributions of behavioral studies to captive management and breeding of rare and endangered mammals.' In Caro, T. (ed.) *Behavioral Ecology and Conservation Biology*. Cary, USA: Oxford University Press, pp. 130-150.

Wiepkema P.R., Koolhaas J.M. (1993) Stress and animal welfare. *Animal Welfare* 2(3): 195-218.

Wormell D., Brayshaw M., Price E., Herron S. (1996) Pied tamarins Saguinus bicolor bicolor at the Jersey Wildlife Preservation Trust: management, behaviour and reproduction. *Dodo Journal of the Wildlife Preservation Trusts* 32: 76-96.