The Effect of Visitors on the Behavior of Zoo-Housed Western Lowland Gorillas (*Gorilla gorilla gorilla*)

Running Title: Effect of Visitors on Gorilla Behavior

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Abstract

Primates, especially apes, are popular with the public, often attracting large crowds. These crowds could cause behavioral change in captive primates, whether positive, neutral, or negative. We examined the impact of visitors on the behavior of six western lowland gorillas (*Gorilla gorilla gorilla*), observing the troop over six weeks during high season (4.5 hours per day, 35 days, May – July 2016). We used focal scan sampling to determine activity budget and enclosure usage, and focal continuous sampling to identify bouts of anxiety-related behavior (visitor-directed vigilance, self-scratching and aggression). Both daily zoo-entry numbers (V_{GATE}) and instantaneous crowds at the exhibit ($V_{DENSITY}$) were measured. Overall, V_{GATE} had little effect across behaviors. However, consistent with the more acute time-frame of measurement, $V_{DENSITY}$ was a better predictor of behavior; at high crowd volumes we observed significant group level changes in activity budget (increased inactivity, increased locomotion, decreased environment-related behaviors), increase in some anxiety-related behaviors and decreased enclosure usage. Although contributing similar effects, it could not be determined if crowd numbers, composition or noise most affected the troop, nor any chronic effects of exposure to large crowds. Nevertheless, our findings suggest that measures to minimize the impacts of large crowds at the exhibit would be beneficial. Furthermore, we highlight potential discrepancies between common methods for measuring visitor numbers: V_{GATE} is less sensitive to detecting visitor effects on behavioral indices than $V_{DENSITY}$. Future studies should appropriately match the biological time-frame of welfare indicators and visitor measures used to ensure reliability of findings.

Keywords: Animal Welfare, Behavior, *Gorilla gorilla gorilla*, Visitors, Western Lowland Gorilla

Introduction

Admitting members of the public allows zoos to educate them on the importance of conservation and animal welfare, and allows people to connect with animals (Fernandez, Tamborski, Pickens, & Timberlake, 2009). However, visitors present an extended, non-natural stimulus for animals, varying in terms of number, noise and activity (Fernandez et al., 2009; Quadros, Goulart, Passos, Vecci, & Young, 2014). Understanding the impact of this stimulus, whether positive, negative or neutral, is essential to making appropriate management decisions for animals in zoological collections.

Primates, especially apes, are popular with the public and can draw large crowds. In response to this, studies of non-human primates make up a large proportion of the current research on visitor effects (Fernandez et al., 2009). Some studies find that visitors are largely ignored by zoo primates (Ross, Wagner, Schapiro, & Hau, 2010), whilst others report that visitors are a beneficial source of enrichment, with animals motivated to positively interact with the public (Cook & Hosey, 1995; Sherwen & Hemsworth, 2019; Webster, 2000). For example, Smith (2014) reported that gorillas (*Gorilla gorilla gorilla*) performed affiliative behaviors, such as approaching and reaching, even with unfamiliar visitors. However, there is mounting evidence that visitors could be a source of stress for primates in captivity (reviewed in Hosey, 2000; Sherwen & Hemsworth, 2019).

Across studies, a number of behavioral changes are reported with increased visitors. Changes in social behavior, most often decreased affiliative and increased aggressive behaviors, are reported in several species (Chamove et al., 1988; Glaston, Geilvoet-Soeteman, Hora-Pecek, & van Hooff, 1984; Kuhar, 2008). Social support, expressed through affiliative interactions, reduces stress in primates (Boccia, Laudenslager, & Reite, 1995; Cheney & Seyfarth, 2009; Judge & Mullen, 2005), suggesting possible secondary effects if these behaviors are reduced. Likewise, increased intragroup aggression can create social instability, with consequent stress (Cheney & Seyfarth, 2009; Judge & Mullen, 2005; Schino & Sciarretta, 2015), and may also increase rates of physical injury (Lambeth, Bloomsmith, & Alford, 1997). Increased locomotion has also been reported (Chamove et al., 1988; Collins & Marples, 2016); whilst some studies interpret this as negative (Collins & Marples, 2016), the overall significance of this increase is unclear. Increases in 'abnormal' or 'stress-related' behaviors with increased visitors have also been found in a number of studies (Carder & Semple, 2008; Clark et al., 2012; Wells, 2005). Decreased enclosure usage at high visitor levels is frequently reported; some find evidence for visitor avoidance (Kuhar, 2008), others find animals approach visitors (positively or negatively) (Hosey & Druck, 1987; Mitchell et al., 1992; Vrancken, van Elsacker, & Verheyen, 1990), although some find no impact (Bonnie, Ang, & Ross, 2016). Changes in behavior may also be impacted by the composition of crowd. For example, children are more likely to actively try to engage and interact with animals (Birke, 2002; Cooke & Schillaci, 2007). The presence of children was associated with greater anxiety-related behaviors in captive gibbons (*Hylobates lar*) although these varied between individuals. Additionally, all animals increased time spent looking towards the audience (from 9% to 36%), suggesting an increase perceived threat (Cooke & Schillaci, 2007), although this has been interpreted as increased attention by other authors (e.g. Sherwen & Hemsworth, 2019; Smith, 2016) and rearing history may have an effect (Sherwen & Hemsworth, 2019).

In gorillas (*Gorilla sp.*), overall evidence for visitor effects and their impact is generally inconclusive; some authors report pronounced responses to large crowd conditions (Carder & Semple, 2008; Wells, 2005), whilst others find little effect (Carder & Semple, 2008; Ross et al., 2010). Discrepancies may result from a number of differences between collections including enclosure design (Davey, 2007; Stoinski, Jaicks, & Drayton, 2012), husbandry styles (Stoinski et al., 2012), habituation (Chamove et al., 1988), and group composition or changes therein (Collins & Marples, 2016). Many studies have small sample sizes, so individual differences in response may be a strong explanatory factor. Sex (Birke, 2002; Stoinski et al., 2012), age (Birke, 2002; Clark et al., 2012), rearing history (Vrancken et al., 1990) and personality (Kuhar, Stoinski, Lukas, & Maple, 2006; Stoinski et al., 2012) can all influence response to stressors. As individuals may be differentially impacted by specific challenges and vary in coping ability (Honess & Marin, 2006), it is important to consider both individual and group level responses to visitors.

A factor of particular note is the measurement of visitor numbers. Two methods are widely reported in the scientific literature: daily evaluation and instantaneous evaluation. Daily evaluation typically uses total daily zoo-entry numbers as a proxy, on the assumption that these will correlate with cumulative visitor numbers at the exhibit (e.g. Kuhar, 2008; Stoinski et al., 2012; Wells, 2005). Instantaneous evaluation determines crowd size at the enclosure simultaneously with the recording of animals' behavior (e.g. Birke, 2002; Carder and Semple, 2008; Cooke and Schillaci, 2007). Although both measures are widely used, little information on how they relate to one another, or comparatively associated with behavioral differences in animals is available. It is possible that they measure different phenomena, explaining some discrepancy in the literature, with implications for determining the appropriate measure to use for different research aims.

Here, we investigated the effect of visitors on a zoo-housed group of western lowland gorillas (*Gorilla gorilla gorilla*). Specifically, we hypothesized that we would see changes in activity budget at high (compared to low) visitor volumes, and if high visitor numbers were perceived negatively, anxiety-related behaviors and aggression would increase, whilst enclosure usage would decrease. These effects were examined at both the group and individual level. Furthermore, two measures of visitor numbers were taken based on zoo-entry numbers and numbers at the exhibit to determine co-relationships between these and gorilla behavior. Since limiting captive animals' exposure to stress is essential for safeguarding their welfare (Kagan, Carter, & Allard, 2015), a key aim of zoos, we focused more strongly on negative impacts.

Methods

Subjects and Housing

Four adult and two infant western lowland gorillas (Table 1) were housed in a large, naturalistic enclosure with access to both indoor and outdoor areas ('Gorilla Kingdom' exhibit at ZSL London Zoo, United Kingdom). The indoor area (120m^2), furnished with ropes, climbing structures, and metal 'nests' fixed to the wall, could be viewed from two windows, each with a standoff barrier preventing visitor approach closer than 1m from the window. The front window was partially obscured by large plants and the side window covered by a twig-like barrier. The outdoor paddock (1600m^2) could be viewed from both a windowed section with a standoff (2m from window), and an open section with a moat protected by a barrier. The outdoor paddock had a large climbing frame in the center, with ~25% of the area planted with pampas grass (*Cortaderia selloana*) cover. Access to the off-exhibit night den was restricted during visitor hours (10:00-18:00). Several other primate enclosures bordered the viewing area on the opposite side of the walkway. The troop is one of the zoo's main attractions, with over 90% of daily visitors passing through the enclosure (Clark et al., 2012). A sign requesting visitors to remain quiet and to refrain from flash photography was located prior to the enclosure entrance.

[Insert Table 1]

Data Collection

Data collection took place for six weeks during May-July 2016, with all days of the week equally represented during the sampling period.

Behavior and Enclosure Use

An ethogram of key behavioral indicators, based on published literature (Table 2 and Table 3; Hoff et al. 1997, Blaney & Wells 2004, Kuhar 2008, Clark et al. 2012), was refined following a pilot study using continuous sampling and discussion with zoo staff, to include 'Infant-directed', 'Infant-cling', 'Infant play' and 'Glass banging'. The enclosure was virtually split into 12 zones (Figure 1), reflecting biologically relevant areas in terms of resources and visibility, based upon known gorilla preferences (Ogden, Lindburg, & Maple, 1993; Ross, Calcutt, Schapiro, & Hau, 2011).

Gorillas were observed from one of two static positions, (Figure 1) dependent on the focal gorilla's location (inside or outside) at the start of the observation. Each individual was observed for a 15-minute focal observation in a random order within each of three observations per day (10:15-12:00, 12:00-13:45, 13:45-15:30) for 35 days, giving 157.5 hours group observation; 26.25 hours per gorilla. Instantaneous focal scans (Martin & Bateson, 2007) at one-minute intervals recorded overall activity (Table 2; interval determined by determining data loss c.f. continuous sampling with the pilot study) and location (Figure 1), whilst continuous focal sampling (Martin & Bateson, 2007) recorded frequency of specific social and anxiety-related behaviors (including stereotypies and abnormal behaviors; Table 3) validated in primate species (gorillas: hair-pluck (Less, Kuhar, & Lukas, 2013; Reinhardt, 2005); other non-human primates: vigilance (Coleman & Pierre, 2014) and self-scratch (Schino, Troisi, Perretta, & Monaco, 1991)) that we predicted to increase if visitor effects were negative. Gorillas were not followed; subjects were recorded as 'Not Visible' once out of sight.

[Insert Table 2 and Table 3]

[Insert Figure 1]

Visitors and Noise

Two measures of visitors were taken. Zoo gate entry numbers (V_{GATE}) represented a proxy for total visitors at the enclosure per day. Visitor density ($V_{DENSITY}$) at the exhibit was recorded using a 6-point scale (adapted from Cooke and Schillaci 2007: Table 4) at each one-minute scan, since counts of individual visitors were not feasible. $V_{DENSITY}$ was measured at the window from which the gorilla was observed i.e. the across the uncovered indoor windows when inside and across all outdoor windows when outside. The observer was always present, so a 'no visitors' category was excluded

(Hosey & Mitchell, 2005). A 5-point scale (Table 4) was used simultaneously to estimate of the proportion of children (defined as people under the age of 16) in the crowd. Where this was uncertain, visitors were conservatively classed as adults.

Sound pressure levels were measured instantaneously at each focal scan using a digital decibel meter (Dr Meter® MS10) from the visitor walkway, 1m from the window at waist height, with the meter pointed towards the enclosure window. The meter uses A-weighting to evaluate sound pressure. We would expect human hearing to closely resemble gorilla hearing, making this weighting appropriate for our study. Noise inside the indoor area (Figure 1) is approximately 10dB lower than this sampling site, with greater attenuation of high frequency noise compared to low (ZSL Internal Report, 2015).

Weather category – bright (few clouds but no visible sun), sun, overcast, windy, rain and heavy rain – and temperature (in $_{o}$C) were recorded at the beginning of each observation session.

[Insert Table 4]

Data Analyses

All statistical analyses were carried out using Rx64 3.6.3. (R Core Team, 2020). A linear model was used to compare V_{GATE} with a daily average of $V_{DENSITY}$ and determine any relationship between these variables. The relationship(s) between immediate crowd variables ($V_{DENSITY}$, proportion of children and noise) were determined, to examine for potential collinearity. A Kendall's tau correlation was used to determine if larger crowds ($V_{DENSITY}$) contained proportionately more children, and the effects of both $V_{DENSITY}$ and children on noise were examined using a first-order autoregressive linear model, to account for visitors remaining over multiple observations (nlme package: Pinheiro et al., 2020). $V_{DENSITY}$ categories of "Ultrahigh Density" and "High Density" were pooled for all analyses.

Due to collinearity, VDENSITY, proportion of children, and noise were examined using separate models in all cases. For behavioral analyses, VGATE numbers were split into five categories – Very Low (<2500 daily visitors), Low (2500-3500), Mid (3501-4500), High (4501-5500), Very High (>5500) – to allow for comparison with results for VDENSITY.

Where the focal individual was not visible, data were excluded from all behavioral analyses. In total, gorilla behaviors were visible for 86.7% of scans (136.55 hours), with a range of 80.9-92.4% (21.24-24.26 hours) for individual gorillas. For all analyses of the effect of instantaneous visitors on behavior, values associated with the 'Observer Only' category were excluded, due to low observation numbers. For analysis of the effect of children on behavior, '0% children' category was excluded due to low observation numbers.

Intra-observer reliability was tested by sampling six recorded focal observations (excluded from the main behavior dataset), immediately, with one recording resampled at the end of each study week. Reliability across weeks was high (Spearman's Correlation: $rho>0.95$, $p<0.03$), and so all observations were used. Some behavior patterns were observed too infrequently to analyze individually and so data were grouped based on the behavior categories shown in Table 2 (Inactivity, Locomotion, Environment, Social, Other). To determine if changes in general activity were associated with visitor numbers, these new categories were then coded for each scan (1=present, 0=absent) to allow easy correction for 'Not Visible' observations. At group level, data were analyzed using Generalized Linear Mixed Effect Models (GLMM, repeated-measure binomial, lmerTest package: Kuznetsovs, Brockhoff, & Christensen, 2017) to examine the effects of VDENSITY, children (categorical), noise (continuous) and VGATE (categorical) on each behavioral category. Across models, individual and session ID were included as random effects. Since weather and temperature were measured on a by session basis, we expect that their effects, as well as the impact of time of day, will be largely accounted for by session ID. Odds ratio (OR), comparing likelihood of behaviours in each category against the baseline (‘Low’) condition, is reported. Differences in individual responses were also analyzed descriptively to aid interpretation.

GLMMs (repeated-measure, zero-inflated Poisson, glmmTMB package: Brooks et al., 2017), with individual and session ID as random factors, were conducted to examine the effects of VDENSITY, children, noise and VGATE on visitor-directed vigilance and self-scratching. Due to the low number of occurrences it was not possible to analyze hair-plucking or conspecific aggression. However, M1 exhibited frequent visitor-directed aggression, which was analyzed for M1 only (repeated-measure, zero-inflated Poisson GLMM, session ID as random factor). Rate ratio, comparing incidence rates of behaviors in each category to the baseline (‘Low’) condition, is reported.

Enclosure usage was determined using a spread of participation index (SPI; Plowman, 2003) with unequal zones to quantify how individuals partitioned their time between defined zones (Figure 1). Enclosure position was recorded for 89.5% of scans (range 81.5-94.5%). SPI-statistics for individual gorillas at different levels of VGATE, VDENSITY, children and noise were calculated. For analysis of the relationship with SPI, noise was grouped into five categories (<60dB, 60-64dB, 65-69dB, 70-74dB, >75dB). At group level, these data were analyzed using a Linear Mixed Model (nlme package) with individual as a random factor.

Results

Relationships Between Visitor Parameters

Visitor density groups, other than ‘Observer’ (2.4%) were similarly represented in the study sample (Low=23.2%, Low-Mid=24.7%, Mid-High=32.2%, High=17.5%). There was a significant, positive association between $V_{DENSITY}$ and V_{GATE}; with higher $V_{DENSITY}$ categories occurring more often on days with higher V_{GATE} (LM: r^2=0.32, $p<0.001$).

Recorded noise ranged from 50-95dB and was very strongly positively associated with both $V_{DENSITY}$ (LME: Observer=REF, Estimate range "Low" – "High" = 5.84-15.56; all $p<0.001$) and proportions of children in the crowd (LME: 0%=REF, Estimate range 1-25% - 76-100% = 4.21-15.95; all $p<0.001$). Average noise levels for each $V_{DENSITY}$ category were as follows: 'Observer' = 55.5dB, 'Low' = 62.2dB, 'Low-Mid' = 65.8dB, 'Mid-High' = 68.9dB, 'High' = 73.06dB, 'Ultra-High' = 76.8dB. However, the sound meter was not calibrated against a research standard noise meter, so although noise levels can be assessed as relative, absolute values reported may not be accurate. High levels of $V_{DENSITY}$ were also associated with proportionately more children (Kendall's Rank Correlation: tau=0.31, $p<0.001$).

Activity Budget

No linear relationship between V_{GATE} categories and any behavioral category was found (Table 5).

When considering instantaneous measures, 'Inactivity' was significantly more likely at 'High' (1.34 times) than 'Low' $V_{DENSITY}$, although it was unaffected by proportion of children in the crowd or noise (Table 5). Similarly 'Locomotion' was significantly more likely at 'High' (1.45 times) than 'Low' $V_{DENSITY}$ and with increasing noise (1.34 times more likely with each additional 10dB), but was unaffected by proportion of children in the crowd (Table 5). Conversely, 'Environment' behaviors were significantly less likely at 'High' (0.42 times) cf. 'Low' $V_{DENSITY}$ and with increasing noise (0.74 times more likely with each additional 10dB), but were unaffected by the proportion of children. (Table 5) 'Social' behaviors did not vary with $V_{DENSITY}$, proportion of children, or noise (Table 5).

[Insert Table 5]

Anxiety-related and visitor-directed behavior

No significant relationship between V_{GATE} and self-scratching was found (Table 6). No linear relationship between visitor-directed vigilance and V_{GATE} was found, although vigilance was more likely (2.04 times) at ‘Mid’ compared to ‘Very Low’ gate numbers (Table 6).

However, when considering instantaneous measures, visitor-directed vigilance was significantly more frequent with increasing $V_{DENSITY}$ (5.71 times more likely to be observed at ‘High’ [calculated rate 0.69 bouts min^{-1}] cf. ‘Low’ [0.06 bouts min^{-1}], Table 6), percentage of children (1.68 times more likely at 76-100% cf. 1-25%, Table 6) and noise (1.63 times more likely with each additional 10dB, Table 6). M1 expressed the maximum rate of vigilance, 2.15 bouts min^{-1}, at ‘High’ $V_{DENSITY}$ showing pronounced increases for crowd sizes above ‘Low-Mid’ densities. Increases in vigilance were seen only in two of the females and to a lesser degree (Figure 2). Self-scratching was also significantly more frequent with increasing $V_{DENSITY}$ (6.24 times more likely to be observed at ‘High’ [0.64 bouts min^{-1}] cf. ‘Low’ [0.09 bouts min^{-1}], Table 6), percentage of children (2.05 times more likely at 76-100% cf. 1-25%, Table 6) and noise (1.79 times more likely with each additional 10dB, Table 6). In all three females, increases in self-scratching at ‘Mid-High’ and ‘High’ densities were observed and maximum self-scratching rate was 1.19 bouts min^{-1}, observed in F1 at ‘High’ $V_{DENSITY}$ (Figure 2).

Similar patterns of effect were seen for proportion of children and noise levels (Table 6).

[Insert Figure 2]

A significant effect of $V_{DENSITY}$ on M1’s visitor-directed aggression was found, with M1’s displays more likely at ‘Mid-High (11.18 times, [0.05 bouts min^{-1}]) and ‘High’ (17.84 times, [0.08 bouts min-

$^{-1}$]) than ‘Low’ [0.01 bouts min^{-1}] $V_{DENSITY}$ (Table 6). Displays were not affected by proportion of children in the crowd or noise. No linear relationship between visitor-directed aggression and V_{GATE} was found.

[Insert Table 6]

Enclosure Use

No linear relationship between V_{GATE} and enclosure usage was found (Table 7).

At group level, enclosure usage was significantly reduced at ‘Mid-High’ and ‘High’ $V_{DENSITY}$ cf. ‘Low’ (Table 7, Figure 3) and with greater noise (categories 60-64dB, 65-69dB, 70-74dB and >75dB cf. reference category <60dB; Table 7).

[Insert Table 7]

Adult gorillas, showed very different patterns of enclosure use according to sex. Where position was known to the observer (90.2% of all observations at ‘Low’ to ‘High’ $V_{DENSITY}$), females spent an average of 72% of time in secluded or difficult to view areas (A, AT, BN, D, E, H: Figure 1) at ‘Low’ $V_{DENSITY}$, cf. 80% at ‘Low-Mid’, 84% at ‘Mid-High’ and 84% at ‘High’. M1 spent less time in hidden areas instead staying in visible areas near the visitor window and other areas near visitors, increasingly with greater $V_{DENSITY}$: 78% ‘Low’ cf. 80% ‘Mid-Low’, 84% ‘Mid-High’ and 88% ‘High’ (Figure 3).

[Insert Figure 3]

Discussion

Overall, we found evidence to support our hypotheses that high visitor numbers affected activity, enclosure use, some anxiety-related and visitor-directed behavior in the gorilla troop compared to low visitor numbers, but only in relation to the crowd size measured at the exhibit. Overall instantaneous visitor numbers were the most consistent predictor of changes in behavior. Unfortunately, where we report similar effects of crowd sizes, proportion of children in the crowd and noise levels in visitor areas on behavior, it was not possible to disentangle their effects due to high collinearity between factors. We therefore discuss only VDENSITY as a proxy for all instantaneous crowd conditions.

Notably, our findings highlight a potential discrepancy between the two most common methods for assessing visitor effects. These methods are rarely examined in tandem and compared. Whilst instantaneous evaluation provides information about the crowds present at the exhibit (e.g. numbers, noise, type), some authors suggest that by evaluating all periods independently of previous crowd conditions, this method fails to take into account cumulative effects of visitors (Kuhar, 2008; Stoinski et al., 2012). Kuhar (2008) proposes that daily averages of both behavior and crowds remove this potential confounder. Here, no linear relationships were found between daily gate numbers and any of the behaviors measured. To accurately represent VGATE, effects on behavior, animals would need to be recorded continuously throughout the entire day to prevent sampling bias and totaled, which often is not considered in other studies (e.g. Kuhar 2008: 30 minutes, twice per day, Stoinski et al. 2012: 1-hour sessions spread across the day). Changes in immediate crowd size are likely to be a much more appropriate explanatory variable for testing predictions regarding acute behavioral changes, particularly where only a small portion of each individual's time can be sampled. Daily totals or averages associated with gate numbers render V_{GATE} less sensitive to detecting potentially key behavioral responses that may reflect avoidance or costs associated with adaptation to visitor presence. This highlights the importance of considering meaningful time-frames in method selection.

Consistent with our predicated change in activity budget, greater inactivity (standing, sitting, lying) was observed in gorillas with exhibit numbers ≥3-4 people deep compared to when gaps between people were still present at the windows. Larger crowd sizes (≥3-4 people deep) were also associated with increased locomotion (climbing, walking, running, swinging) as in other primates (Chamove et al., 1988; Hosey, 2005). No changes in social behaviors relating to crowd sizes were found. In the current troop, the greater inactivity and locomotion were concurrent with collectively less environment-directed behavior (feeding, drinking and manipulation of non-food objects) and a sustained, although small, reduction in enclosure use. Changes in activity budget are difficult to assess in terms of welfare implications as a number of factors, both positive and negative, may impact state behaviors, and may also be influenced by external factors such as time of day and husbandry schedules. Such changes should be taken into account with other indices (Sherwen & Hemsworth, 2019). Our results suggest a shift in time budget with larger crowds, whereby maintenance, object-exploration activities and space use were temporally suppressed, consistent with some other studies of visitor effects on gorillas (Clark et al., 2012; Collins & Marples, 2016).

When examining event behaviors, frequencies of hair-pluck and other abnormal behaviours were too low to formally analyze. However, likelihoods of both visitor-directed vigilance and self-scratching were over 5.5 times greater at visitor densities ≥3-4 people deep compared to when gaps were still present at the windows, consistent with one site reported by Carder and Semple (2008), who used similar instantaneous evaluation of crowd sizes. Although frequently used in studies of visitor effects, the use of vigilance to demonstrate anxiety is not without limitations. Whilst many functions of vigilance in wild primates relate to threat detection and monitoring (Gould, Fedigan, & Rose, 1997;

Kutsukake, 2007; Quenette, 1990; Steenbeek, Piek, & Buul, 1999), it is important to note that the perception of threat in captive-bred and particularly hand-reared primates is likely to be different to those in the wild. In some cases, animals may interact positively or be interested in visitors (Sherwen & Hemsworth, 2019; Smith, 2014; Vrancken et al., 1990), so vigilance may be positive. Indeed, primates have been reported to choose to watch video clips (e.g. Harris et al. 1999; Maloney et al. 2011), although care must be taken in generalizing responses to video and live stimuli due to a number of complexities including video subject (Maloney et al., 2011), and differences in perception of 2D images and 3D events (Leighty, Menzel, & Fragaszy, 2008). Some authors (e.g. Clark et al. 2012) have tried to separate visitor-directed vigilance into positive and negative categories and, moving forwards, rigorous definition of these differences could help to improve interpretation of vigilance. However, in spite of these limitations, it is likely that negative visitor vigilance would be correlated with other behavioral factors. Indeed, Clark et al. (2012) suggested negative visitor vigilance was likely to be associated with visitor-directed aggression, a pattern that we see in our data (discussed later). Self-scratching is well-validated as a behavioral sign of anxiety in several other primate species (Castles, Whiten, & Aurelli, 1999; Maestripieri, 1993; Schino, Rosati, Geminiani, & Aureli, 2007; Schino et al., 1991), making it a useful tool for indicating short-term welfare status. Importantly in our study the correspondence of these two measures strengthens the interpretation of greater vigilance as negative in this context.

Clark *et al.* (2012) previously studied the same troop, reporting increased negative visitor vigilance with noise, which we found to be indistinguishable from $V_{DENSITY}$, and decreased environmental behaviors with higher crowd sizes at the exhibit, as in our study. However, these changes did not correspond with parallel changes in fecal glucocorticoid metabolites. Consistent with our findings, total daily visitors did not significantly impact the behavior of the three gorillas. As with our study, this may be related to the sampling period; gorillas were observed for a single session (1 hour) per day. Although our results have some similarities to those of Clark *et al.* (2012), it is important to note that major group changes have occurred making direct comparisons difficult. Both the presence of a new dominant male and the birth of two infants could alter troop behavior (Collins & Marples, 2016).

Gorillas were selective in their use of space, even at 'Low' crowd conditions. This is not uncommon; Ross *et al.* (2011) found that gorillas were highly selective in their use of space, spending >50% of time in only 1.5% of their available area. Although an overall effect of visitors on enclosure usage was found in our study, whilst acknowledging a very small sample size is unlikely to be representative, differences between individuals and sexes were apparent. In keeping with social roles, the male responded with approach and active displays of visitor-directed aggression whereas females responded more passively with avoidance. Despite these differences, behavioral indices of short-term anxiety associated with high-density visitors were observed in both sexes. At exhibit crowds ≥2-3 people deep, females chose areas further from crowds or with reduced or no visitor visibility, consistent with Kuhar (2008) suggesting avoidance of visitors. Although further into cover, self-scratching, descriptively performed more by the females, was still more frequent with higher crowds at the enclosure, suggesting the potential buffering the effects of cover on visitors (Davey, 2007) was not sufficient to prevent greater anxiety. In contrast, the male more frequently positioned himself in front of the visitor window when the exhibit was busy and showed relatively higher rates of vigilance. Conflicting with our findings, Bonnie, Ang, & Ross, (2016) found that gorillas did not alter their use of areas near to visitors, however potential sex differences which may have counter-balanced each other were not taken into account. The contrast between males and females may be explained by different roles in the social group, with the male as the protector (Taylor & Goldsmith, 2003). We might expect male vigilance is a normal part of this role, but despite little information on what rates are normal, the relative increase within M1 in association with visitor density is potentially of note. Aggression between conspecifics was rare (<1% of observations), so we were unable to determine the impact of visitor density. However, visitor-directed aggression shown by the male increased more than tenfold with a crowd ≥2-3 people deep compared to when gaps at the windows were visible. Visitor-directed aggression is reportedly common among captive primates (e.g. Mitchell *et al.* 1991).

Aggressive displays are a natural species-specific behavior, particularly for silverback males (Stokes, 2004). However, there is little information available on the rate at which these behaviors are appropriate, especially in the captive setting. Although not formally recorded, aggressive displays by M1 were met by large crowd reactions and attracted new visitors, potentially creating a positive feedback loop between aggression and $V_{DENSITY}$. If the male's response is consistently ineffective in mitigating threats, it could contribute to increased frustration and a chronic negative state. As well as potentially increasing crowd densities, females observing aggressive displays by the male may be negatively affected, increasing female anxiety-related behaviors, as seen among wild primates (Schino & Sciarretta, 2015).

It is difficult to assess the impact of visitors without a full understanding of how deviations in behavior, particularly those in activity budget, are significant for welfare and at what magnitude these deviations become problematic (Howell & Cheyne, 2019; Sherwen & Hemsworth, 2019). A number of abnormal behaviours (such as hair-plucking) and intragroup aggression occurred at frequencies too low to assess with regards to crowd size and no decrease in affiliative social behaviours, often used to indicate positive welfare (Sherwen & Hemsworth, 2019), with high crowds were reported. However, the collective alteration of observed changes in time budget, some anxiety-related behavior and enclosure use with increasing crowds indicates that high densities of visitors at the exhibit (2-3 people deep and above) may be a negative stimulus for the troop that we investigated.

Since a number of extrinsic (e.g. management, enclosure design) and intrinsic (e.g. group dynamics) factors can impact gorilla behavior (Stoinski et al., 2012), making generalizations from a single institution over a relatively short time period should be avoided. Although evidence from previous studies is conflicting, potentially due to methodological differences, the similarity of our findings with those of others (Carder & Semple, 2008; Collins & Marples, 2016; Kuhar, 2008) still highlights the potential for broader trends across collections. To allow for appropriate management to mitigate visitor effects, there is a need for systematic evaluation across collections to determine if common patterns exist and how other factors may contribute. The present study highlights the need for (i) further research to disentangle visitor-related variables such as type, behavior, noise levels and time of day effects to help target management interventions; (ii) choice of methods of measuring visitor numbers appropriate to the time-frame for the outcome indices measured; and (iii) investigation at the individual level due to variation in response pattern to visitors (e.g. sex differences).

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Tables

Table 1: Characteristics of gorillas housed in a single troop at ZSL London Zoo’s Gorilla Kingdom

ID	**Alias**	**Sex**	**Age**	**Rearing History**
Female 1	F1	Female	22	Captive/Hand
Female 2	F2	Female	17	Captive/Parent
Female 3	F3	Female	42	Captive/Hand
Male 1	M1	Male	19	Captive/Hand
Infant 1	I1	Female	1	Captive/Parent
Infant 2	I2	Male	7 months	Captive/Parent

Table 2: Ethogram of gorilla behaviours recorded using focal instantaneous scan sampling in this study. Based largely on the work of Clark *et al.* (2012) and revised through pilot studies.

Behavior category	Behavior	Description
Inactive	Lie	Gorilla is reclining with little or no weight on hands and feet.
	Sit	All or most of gorilla's weight is placed on the buttock.
	Stand	Gorilla has all weight placed on limbs, either on all fours or hindlimbs.
Locomotion	Walk	Gorilla is moving terrestrially at a slow pace on all fours or hindlimbs.
	Run	Gorilla is moving terrestrially at a fast pace on all fours or hindlimbs.
	Climb	Gorilla is moving using climbing structures, at least three limbs off the ground
	Swing	Gorilla is moving suspended from the climbing structures or roof using forelimbs only, hindlimbs off the ground.
Environment	Feed	Food is placed in the mouth and does not reappear. Can occur in lying (L), sitting (S) or standing (St) position
	Forage	Movement of gaze or hands over areas where food is present, or manipulation of food items. Can occur in lying (L), sitting (S) or standing (St) position.
	Drink	Gorilla places water (or other ingestible drink) in mouth without it reappearing. Can occur in lying (L), sitting (S) or standing (St) position.
	Object	Gorilla is manipulating a non-food, non-social object. Can occur in lying (L), sitting (S) or standing (St) position.
Social	Allogroom	Gorilla is grooming or being groomed by a conspecific. Hand or foot movement so that fingertips are drawn through the fur of another individual. Gorillas can be instigator (I) or recipient (R)
	Play	Gorilla is engaged in social play with a conspecific. Displays behaviours associated with normal social interactions (aggression, sexual) which are exaggerated/out of context (Vanderschuren, Niesink, & Van Pee, 1997).
	Infant Play	Adult gorilla is engaged in play (as defined above) with an infant. Behaviour can only be performed by adult gorillas.
	Infant-directed	Adult gorilla is engaged in a non-play infant related behaviour. May include suckling, cuddling. Behaviours can only be performed by adult gorillas.
	Infant Cling	Infant gorilla is grasping the fur of an adult. Behavior can only be performed by infant gorillas.
	Sexual	Gorilla is involved in mating-related behaviours, including mounting and courtship displays.
Other		Gorilla is engaged in a behaviour not covered by any of the above categories
Not visible		Gorilla not visible to observer

Table 3: Ethogram of gorilla behaviours recorded using focal continuous sampling for this study and the predicted change in these behaviors if visitors are perceived as a negative stimulus by gorillas. Based largely on the work of Clark *et al.* (2012) and revised through pilot studies.

Behavior	Description	Predicted change
Self-scratch	Hand or foot is moved such that fingertips are repeatedly drawn through the fur. A single bout of self-scratching ends when the repeated movement is ceased for two or more seconds.	**Increase** (Schino *et al.* 2007; Castles *et al.* 1999; Polizzi *et al* 2012; Schino *et al.* 1991)
Hair-pluck	Recurrent hair pulling using fingers or teeth. Removal of hair seen by observer. May be followed by ingestion of hair. A single bout ends when the movement is ceased for two or more seconds.	**Increase** (Less *et al.* 2013; Reinhardt 2005)
Visitor-directed vigilance	Gorilla is alert, with gaze fixed on the public. May include interaction e.g. through direct eye contact. A single bout ends when the gorilla looks away from the crowd.	**Increase** (Birke, 2002; Watts, 1998)
Aggression	Gorilla is engaged in an aggressive display, either contact or non-contact with a conspecific. May include baring teeth, beating chest, calling hitting, charging, throwing objects, raising hair. Gorilla can be an Instigator (I) or a recipient (R)	**Increase** (Lambeth *et al.* 1997; Judge and Mullen 2005; Sherwen *et al.* 2015)
Visitor-directed aggression	Gorilla is engaged in an aggressive display directed towards the public. May include glass banging, baring teeth, beating chest, calling, charging, throwing objects, raising hair. Gorilla can only be an instigator (I).	**Increase** ((Mitchell *et al.* 1991; Birke 2002)

Table 4: Categories used for scoring visitor density (modified from Cooke and Schillaci (2007)) and percentage of children at the 'Gorilla Kingdom'.

	Condition	**Definition**
Visitor Density	Observer Only	Only the observer is present at the focal windows. Visitors may be elsewhere in the building not viewing the gorillas.
	Low Density	Visitors present. Gaps still seen at focal viewing windows
	Low-Mid Density	No gaps seen at focal windows. Audience no more than one person deep
	Mid-High Density	Audience is 2-3 people deep. No gaps at focal windows
	High Density	Audience 3-4 people deep. No gaps at focal windows
	Ultra-High Density	Audience ≥4 people deep. No gaps at focal windows
Presence of Children	0	No children present in audience
	1	1-25% of audience members are children
	2	26-50% of audience members are children
	3	51-75% of audience members are children
	4	76-100% of audience members are children

Table 5: Results of generalized linear mixed-effect models examining behavioural categories (proportion of scans) in relation to visitor density, proportion of children, noise and gate numbers. Significant differences from the reference category are signaled by * and in bold.

	Inactivity					**Locomotion**				
	OR†	CI‡	p-value	Mean	SD§	OR	CI	p-value	Mean	SD
Visitor Density										
Low	REF¶	REF	REF	0.52	0.50	REF	REF	REF	0.11	0.32
Low-Mid	1.14	0.94-1.39	0.178	0.54	0.50	0.83	0.65-1.07	0.148	0.10	0.29
Mid-High	1.14	0.94-1.40	0.190	0.58	0.49	0.99	0.76-1.28	0.931	0.10	0.30
High	**1.34**	**1.05-1.70**	**0.017***	**0.62**	**0.48**	**1.45**	**1.07-1.95**	**0.015***	**0.12**	**0.32**
Children										
1-25%	REF	REF	REF	0.56	0.50	REF	REF	REF	0.10	0.30
26-50%	0.87	0.74-1.03	0.098	0.55	0.50	1.05	0.85-1.30	0.629	0.10	0.30
51-75%	0.97	0.78-1.20	0.762	0.57	0.50	1.10	0.83-1.45	0.503	0.10	0.30
76-100%	1.01	0.80-1.28	0.947	0.56	0.50	1.23	0.92-1.65	0.162	0.11	0.31
Noise	1.00	0.99-1.01	0.960	0.56	0.50	**1.03**	**1.01-1.04**	**<0.001**	**0.10**	**0.31**
Gate Numbers										
Very Low	REF	REF	REF	0.59	0.49	REF	REF	REF	0.11	0.31
Low	0.81	0.47-1.39	0.445	0.57	0.50	1.21	0.70-2.08	0.490	0.12	0.32
Mid	**0.64**	**0.41-0.99**	**0.044***	**0.53**	**0.50**	0.91	0.58-1.42	0.665	0.10	0.29
High	0.71	0.42-1.18	0.183	0.57	0.49	1.09	0.65-1.83	0.731	0.10	0.30
Very High	0.77	0.45-1.32	0.345	0.58	0.49	1.38	0.80-2.35	0.243	0.11	0.31

	Social					**Environment**				
	OR	CI	p-value	Mean	SD	OR	CI	p-value	Mean	SD
Visitor Density										
Low	REF	REF	REF	0.22	0.41	REF	REF	REF	0.15	0.36
Low-Mid	1.04	0.81-1.34	0.752	0.24	0.42	0.89	0.68-1.18	0.425	0.13	0.34
Mid-High	0.99	0.76-1.29	0.969	0.21	0.41	0.76	0.57-1.03	0.073	0.11	0.31
High	0.82	0.59-1.14	0.236	0.17	0.38	**0.42**	**0.29-0.61**	**<0.001***	**0.07**	**0.26**
Children										
1-25%	REF	REF	REF	0.21	0.40	REF	REF	REF	0.13	0.33
26-50%	1.05	0.85-1.29	0.663	0.21	0.41	1.19	0.94-1.50	0.156	0.12	0.33
51-75%	0.97	0.73-1.28	0.818	0.22	0.41	0.93	0.67-1.29	0.667	0.11	0.31
76-100%	0.91	0.67-1.23	0.532	0.23	0.42	0.73	0.51-1.06	0.096	0.09	0.28
Noise	0.99	0.97-1.01	0.220	0.21	0.41	**0.97**	**0.96-0.99**	**0.008***	**0.12**	**0.32**
Gate Numbers										
Very Low	REF	REF	REF	0.20	0.40	REF	REF	REF	0.09	0.29
Low	0.74	0.37-1.49	0.401	0.18	0.39	1.62	0.59-4.41	0.347	0.12	0.33
Mid	1.50	0.86-2.62	0.152	0.23	0.42	2.05	0.91-4.63	0.083	0.13	0.34
High	1.80	0.94-3.44	0.074	0.22	0.42	1.53	0.60-3.92	0.375	0.09	0.29
Very High	0.80	0.40-1.62	0.533	0.18	0.38	1.44	0.53-3.91	0.473	0.13	0.34

†Odds Ratio, ‡Confidence Interval, §Standard Deviation, ¶Reference Category

Table 6: Results of generalized linear mixed-effect models examining anxiety-related behaviours (rate) in relation to visitor density, proportion of children, noise and gate numbers. Significant differences from the reference category are signaled by * and in bold.

	Self-Scratch					**Vigilance**				
	RR	CI	p-value	Mean	SD	RR	CI	p-value	Mean	SD
Visitor Density										
Low	REF	REF	REF	0.09	0.32	REF	REF	REF	0.06	0.27
Low-Mid	**1.45**	**1.16-1.80**	**<0.001***	**0.12**	**0.38**	**1.47**	**1.12-1.92**	**0.005***	**0.08**	**0.35**
Mid-High	**3.53**	**2.90-4.30**	**<0.001***	**0.34**	**0.67**	**3.38**	**2.64-4.33**	**<0.001***	**0.28**	**0.74**
High	**6.24**	**5.09-7.64**	**<0.001***	**0.64**	**0.99**	**5.71**	**4.44-7.36**	**<0.001***	**0.69**	**1.25**
Children										
1-25%	REF	REF	REF	0.22	0.55	REF	REF	REF	0.19	0.61
26-50%	**1.20**	**1.07-1.35**	**0.002***	**0.29**	**0.64**	1.05	0.93 -1.20	0.418	0.27	0.76
51-75%	**1.61**	**1.39-1.86**	**<0.001***	**0.40**	**0.79**	**1.27**	**1.08-1.49**	**0.003***	**0.34**	**0.83**
76-100%	**2.05**	**1.77-2.38**	**<0.001***	**0.52**	**0.93**	**1.68**	**1.43-1.99**	**<0.001***	**0.52**	**1.17**
Noise	**1.06**	**1.05-1.07**	**<0.001***	**0.29**	**0.66**	**1.05**	**1.04-1.05**	**<0.001***	**0.26**	**0.77**
Gate Numbers										
Very Low	REF	REF	REF	0.31	0.68	REF	REF	REF	0.22	0.71
Low	0.85	0.54-1.32	0.464	0.29	0.69	1.00	0.58-1.74	0.990	0.28	0.84
Mid	0.84	0.58-1.20	0.329	0.27	0.64	**2.04**	**1.32-3.14**	**0.001***	0.30	0.82
High	0.81	0.53-1.23	0.318	0.29	0.66	1.16	0.69-1.93	0.577	0.23	0.67
Very High	0.88	0.57-1.37	0.583	0.28	0.64	1.66	0.99-2.80	0.057	0.23	0.66

	Visitor-Directed Aggression (M1)				
	RR	CI	p-value	Mean	SD
Visitor Density					
Low	REF	REF	REF	0.01	0.07
Low-Mid	4.42	0.50-39.01	0.181	0.02	0.16
Mid-High	**11.18**	**1.42-88.13**	**0.022***	**0.05**	**0.26**
High	**17.84**	**2.22-143.13**	**0.007***	**0.08**	**0.36**
Children					
1-25%	REF	REF	REF	0.03	0.16
26-50%	0.55	0.21-1.44	0.223	0.02	0.14
51-75%	1.98	0.74-5.34	0.175	0.09	0.43
76-100%	1.79	0.66-4.89	0.255	0.12	0.40
Noise	1.05	1.00-1.10	0.074	0.05	0.26
Gate Numbers					
Very Low	REF	REF	REF	0.11	0.40
Low	0.54	0.10-2.98	0.479	0.08	0.37
Mid	0.59	0.15-2.35	0.454	0.04	0.23
High	**0.05**	**0.00-0.60**	**0.019***	**0.00**	**0.06**
Very High	0.12	0.01-1.02	0.053	0.01	0.10

†Rate Ratio, ‡Confidence Interval, §Standard Deviation, ¶Reference Category

Table 7: Results of generalized linear mixed-effect models examining changes in enclosure usage (measured by Spread of Participation Index values). Significant differences from the reference category are indicated with * and in bold.

	Enclosure Usage			
	Coefficient	p-value	Mean	SD†
Visitor Density				
Low	REF‡	REF	0.70	0.15
Low-Mid	0.06	0.088	0.76	0.10
Mid-High	**0.13**	**0.001***	**0.83**	**0.07**
High	**0.15**	**<0.001***	**0.85**	**0.06**
Children				
1-25%	REF	REF	0.77	0.10
26-50%	0.05	0.079	0.81	0.06
51-75%	0.04	0.087	0.81	0.07
76-100%	0.05	0.069	0.81	0.09
Noise (dB)				
<60	REF	REF	0.68	0.16
60-64	**0.08**	**0.033***	**0.76**	**0.11**
65-69	**0.12**	**0.003***	**0.80**	**0.07**
70-74	**0.15**	**<0.001***	**0.82**	**0.07**
>75	**0.18**	**<0.001***	**0.85**	**0.08**
Gate Numbers				
Very Low	REF	REF	0.87	0.06
Low	-0.07	0.071	0.80	0.09
Mid	**-0.12**	**0.006***	**0.75**	**0.11**
High	**-0.10**	**0.021***	**0.78**	**0.11**
Very High	-0.06	0.141	0.81	0.12

†Standard Deviation, ‡Reference Category

Figure Legends

Figure 1: Enclosure diagram showing the zones used, labeled A-J. Indoor areas: A=Nest back, AT=Nest back top, B=Indoor Front, BN=Front nest, C=Visitor near, D=Nest hidden, E=Indoor screened, Outdoor areas: F=Climbing frame, G=Outdoor window, H=Outdoor hidden, I=Outside standoff, J=Cave. Stars represent the two possible observation locations. Indoor area is labeled 'Day Gym' and outdoor area is labeled 'Gorilla Paddock'.

Figure 2: Rates of vigilance and self-scratch behaviors (bouts per minute) for individual gorillas at different categories of visitor density.

Figure 3: Relationship between spread of participation index (SPI) and Visitor density. Values closer to 1.0 represent use of fewer areas.

Legend: Female 1 (F1), Female 2 (F2), Female 3 (F3), Infant 1 (I1), Infant 2 (I2), Male 1 (M1)