



---

# How is Western Lowland Gorilla (*Gorilla gorilla gorilla*) Behavior and Physiology Impacted by 360° Visitor Viewing Access?

Maire O'Malley<sup>1,2</sup>, Jocelyn M. Woods<sup>1,3</sup>, Jocelyn Byrant<sup>1</sup>, and Lance J. Miller<sup>1,\*</sup>

<sup>1</sup>Animal Welfare Research, Chicago Zoological Society

<sup>2</sup>The Dian Fossey Gorilla Fund International

<sup>3</sup>Department of Animal and Dairy Sciences, University of Wisconsin-Madison

\*Corresponding author (Email: [Lance.Miller@czs.org](mailto:Lance.Miller@czs.org))

**Citation** – O'Malley, M., Woods, J.M., Byrant, J., & Miller, L.J. (2021). How is Western lowland gorilla (*Gorilla gorilla gorilla*) behavior and physiology impacted by 360° visitor viewing access? *Animal Behavior and Cognition*, 8(4), 468-480. <https://doi.org/10.26451/abc.08.04.02.2021>

**Abstract** – The effect visitors may have on the welfare of professionally managed animals is vital to consider. The present study utilized an experimental approach to examine how 360° visitor viewing access (i.e., viewing from all sides of the habitat) impacts the behavior and physiology of Western lowland gorillas (*Gorilla gorilla gorilla*,  $N = 7$ ). Data collection included behavioral observations and obtaining fecal samples to examine physiological indicators of welfare. The study included a baseline period observing the gorillas' behavior and physiology during the typical 360° visitor viewing access and a treatment period examining the same indicators but reducing viewing access by approximately 70%. Behavioral states, behavioral events, and hormone data were compared across conditions using Wilcoxon signed-rank tests. Restricted viewing did not impact social or solitary grooming (as a state behavior), social or solitary play, foraging, stereotypies, locomotion, inactivity, or behavioral diversity. However, restricted viewing significantly reduced solitary grooming events, fecal glucocorticoid metabolites, and the ratio of glucocorticoid metabolites to dehydroepiandrosterone metabolites. These results suggest that 360° visitor viewing access may have an impact on the welfare of gorillas. However, further research is necessary to thoroughly understand the influence of allowing 360° visitor viewing on behavior and its possible interaction with variables of the zoo environment.

**Keywords** – Animal welfare, Dehydroepiandrosterone metabolites, Glucocorticoid metabolites, Social behavior, Visitor effect, Zoo

---

Animal welfare is a priority of institutions accredited by the Association of Zoos and Aquariums (AZA). Animal welfare researchers must consider many variables, including the animal's behavior, physiology, and the details of the animal's environment (Hosey, 2005). An environmental variable that has received a great deal of attention is the presence of visitors. The effect of visitors has long been studied to measure welfare across many species, most commonly among nonhuman primates (Hosey, 2005; Hosey et al., 2016). Although numerous visitor effect studies have been published to date, there is still a need for a deeper understanding of how specific variables related to visitor presence influence individual animal welfare (Davey, 2007; Fernandez et al., 2009; Hosey, 2000; Sherwen & Hemsworth, 2019).

In visitor effect research, some of the most common variables of focus are visitor presence (Chamove et al., 1988; Collins et al., 2017), crowd size (Bonnie et al., 2016; Kuhar, 2008), visitor noise levels (Cooke & Schillaci, 2007; Hashmi & Sullivan, 2020; Quadros et al., 2014), visitor behavior (Nimon & Dalziel, 1992; Woods et al., 2019), and visitor proximity to the habitat or the animals (Bitgood et al.,

1988; Choo et al., 2011; Miller et al., 2019). While the body of visitor effect literature is continually expanding, findings are typically broad and often conflicting. In an early study, Hosey and Druck (1987) examined 12 nonhuman primate species under five crowd conditions ranging from no visitors to large, active groups. They discovered that the subjects directed behaviors toward the crowd in all conditions, in the form of threat displays, food-begging, and submissive behaviors, causing the authors to question whether professionally managed primates can become fully habituated to visitor presence. However, recent studies challenge this idea, with results suggesting that visitors may not have a significant impact on primate behavior (Collins et al., 2017; Goodenough et al., 2019; Hansen et al., 2020; Hosey et al., 2016; Todd et al., 2007). For example, Hosey and colleagues (2016) analyzed the impact of visitor numbers on wounding rates in chimpanzees (*Pan troglodytes*) and ring-tailed lemurs (*Lemur catta*). They discovered that rising visitor numbers were not associated with wounding rates in either species. It is clear that determining which variables of visitor presence impact animal behavior, if at all, is complex and requires further in-depth investigation.

Western lowland gorillas (*Gorilla gorilla gorilla*) are a commonly studied focal species. Past research has examined the relationship between gorilla welfare and variables such as behavior directed toward guests by gorillas (Clark et al., 2012), assessment of gorilla personality (Stoinski et al., 2012), high and low crowd conditions (Kuhar, 2008), daily visitor attendance and visitor density (Lewis et al., 2020), and the incorporation of visual barriers to restrict visitor viewing access (Blaney & Wells, 2004). However, compared to other variables regularly considered, visitor viewing access has not gained sufficient attention (Bloomfield et al., 2015). Two studies that utilized visual barriers attached to the visitor viewing windows at gorilla habitats found a significant reduction in the display of stereotypic and aggressive behaviors (Blaney & Wells, 2004) and a decrease in vigilance in two-thirds of a gorilla troop (Clark et al., 2012). Studies that have restricted visitor viewing in species other than gorillas reported an increase in reproductive success and reductions in fear, stress-related behaviors, and cortisol concentrations (Carlstead et al., 1999; Chamove et al., 1988; Chiew et al., 2019, 2020; Davis et al., 2005; Sherwen, Harvey, et al., 2015; Sherwen, Magrath, et al., 2015). However, contrasting results suggest that visual barriers may or may not enhance welfare (Bloomfield et al., 2015; Martín et al., 2016). Conflicting results in zoo research are inevitable due to habitat variability and design, group dynamics, and environmental conditions, but accounting for as many variables as possible could help determine which factors may be most influential (Hosey, 2005).

Utilizing multiple indicators of welfare when conducting research is considered best practice (Whitham & Wielebnowski, 2013). Physiological indicators are becoming increasingly popular, particularly hormonal measures of the adrenal system (Broom & Johnson, 1993; Möstl & Palme, 2002). A common approach to studying the functionality and activation of the hypothalamic-pituitary-adrenal (HPA) axis is evaluating glucocorticoid metabolites through non-invasive fecal samples (Touma & Palme, 2005). Previous research on adrenal activity revealed that urinary glucocorticoids correlate with hair-plucking bouts among bonobos (*Pan paniscus*, Brand et al., 2016). A study focusing on black rhinos (*Diceros bicornis*) found that more extensive perimeter walkways around a habitat increased the rhinos' fecal glucocorticoid metabolite concentrations (Carlstead & Brown, 2005). Although the analysis of fecal glucocorticoid metabolites can be valuable, it is not always the most reliable tool to interpret adrenal activity since positive or negative stressors can trigger the HPA axis (Palme, 2019; Whitman & Wielebnowski, 2013; Whitman et al., 2020; Wielebnowski & Watters, 2007). Whitman and colleagues (2020) discuss using the ratio of glucocorticoid metabolites to dehydroepiandrosterone (DHEA) metabolites as a better way to examine adrenal function. The analysis of cortisol:DHEA may provide a more complete picture of how the HPA axis performs and indicates physiological imbalance within the endocrine system (Whitman et al., 2020). It is thought that the examination of cortisol:DHEA is a clear indicator of stress considering the adversarial relationship between cortisol and DHEA primary physiological functions (Kamin & Kertes, 2017). While the cortisol:DHEA ratio has mainly been utilized in human studies, research among nonhuman animals is expanding, providing support that cortisol:DHEA may be a viable measure of long-term stress (Whitham et al., 2020).

The current study aimed to investigate the visitor effect on zoo-housed gorillas, which, in turn, may influence future habitat design for Western lowland gorillas and other zoo-housed species. Specifically, we

examined the impact of 360° visitor viewing on gorilla welfare by collecting behavioral and physiological data before and after restricting public viewing access to the habitat. To our knowledge, this is the first study to manipulate visitor viewing access that encompasses the entire circumference of a gorilla habitat.

## Method

### Subjects and Housing

The study subjects were seven Western lowland gorillas consisting of four adults, two juveniles, and one infant within a family troop housed at the Chicago Zoological Society's Brookfield Zoo (Table 1). The gorillas were socially housed in an approximately 332 m<sup>2</sup> habitat (Northside: ~9 m; Eastside: ~24 m; Southside: ~25 m; Westside: ~27 m) within Tropic World (Figure 1). Tropic World encompasses three exhibit segments (South America, Asia, and Africa), which the guests must walk through upon entering. The single visitor entrance is at the South American exhibit, leading guests along a single pathway to Asia and eventually Africa, where the gorillas are housed. The exit is at the northeast corner of the gorilla habitat.

**Table 1**

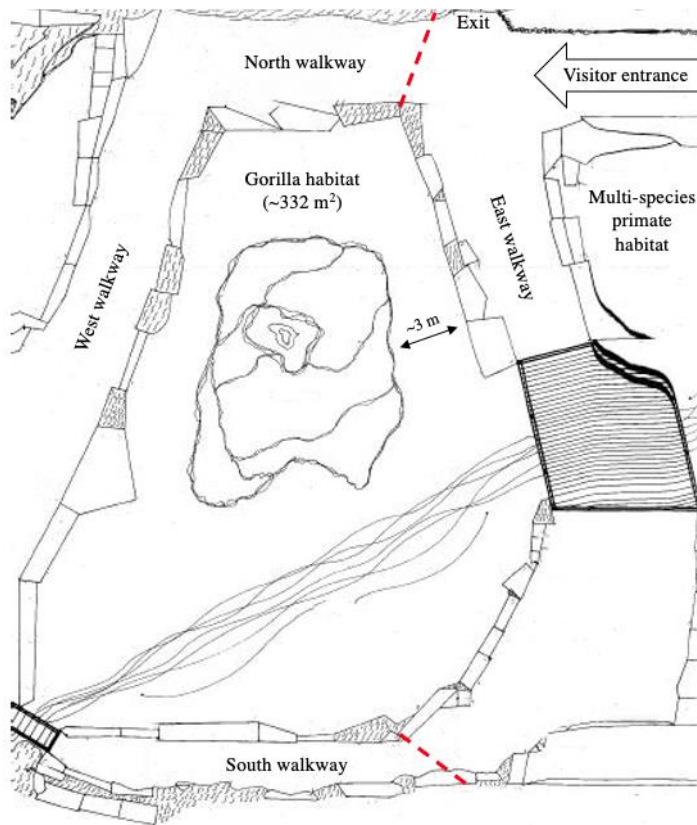
*Subjects of the Current Study, Including Sex and Age at the Time of the Study*

Subject	Sex	Age (years)
G1	Male	39
G2	Female	31
G3	Female	24
G4	Female	15
G5	Female	5
G6	Male	4
G7	Female	1

The gorilla habitat is unique in that visitors are allowed 360° viewing access (i.e., the ability to view from all sides of the habitat). The moat wall, which serves as the only physical barrier between the gorillas and visitors, ranges from approximately 4 to 8 m in height and is approximately 3 m in width. The habitat includes an artificial waterfall that flows into a river, large rock structures, artificial tree structures, and natural and artificial vegetation. Various species of African-native birds have free-range access throughout the building. A habitat with black-and-white colobus (*Colobus angolensis*), Allen's swamp monkeys (*Allenopithecus nigroviridis*), and red-tailed guenons (*Cercopithecus ascanius*) is visually adjacent to the gorilla habitat. The gorillas were given daily habitat access from 10:00 – 16:15. They were shifted into holding for a short time (~10 min) at noon for positive reinforcement training. They had *ad libitum* access to water and environmental enrichment throughout the day and received a variably-timed mid-day scatter feed.

### Behavioral Data Collection

The study was conducted over six weeks (September to November 2019). The six-week study period was broken into two three-week conditions consisting of a baseline and treatment period where gorillas had full access to their habitat at all times. During the baseline period, visitors had 360° viewing access allowing them to observe the gorillas around the entire circumference of the habitat. Immediately following the baseline period was a three-week treatment where the visitors were restricted access by approximately 70% of the total perimeter (estimated by actual habitat measurements). Restriction resulted in visitors viewing the gorillas only from the East walkway. The perimeter walkway was barricaded at the start of the North and South walkways, completely blocking off the North, South, and West viewing areas (see Figure 1 for the location of the barriers).

**Figure 1***Gorilla Habitat Map*

*Note.* Red dashed lines demonstrate where the barriers were placed.

Behavioral data were collected through the ZooMonitor application (Wark et al., 2019) on handheld iPads by two trained observers. The observers achieved inter-observer reliability of greater than 80% agreement (Shweta et al., 2015; Landis & Koch, 1977) for behavioral states and events. Each observation consisted of a ten-minute focal follow, using instantaneous sampling (behavioral states) every sixty seconds and all occurrence sampling (behavioral events). All behaviors that were recorded are listed in the ethogram presented in Table 2. Bouts of aggression were recorded very rarely during observations (< 5 bouts across all individuals) and were excluded from statistical analyses. All observations were conducted from the East walkway (see Figure 1), which was accessible to visitors in both conditions. Observations were conducted on most weekdays between the hours of 10:00 and 16:15. A pseudo-randomized, counterbalanced schedule was followed to determine which individual would be observed at which time throughout the study. Individuals were recorded as not visible if the observer could not see the individual from the East walkway, regardless of whether the individual was in the off display holding area or visually obstructed on habitat.

### ***Attendance***

Daily visitor numbers were collected from the Chicago Zoological Society's attendance records to provide additional insight into visitor flow. Total visitor numbers per day were utilized to calculate the median and interquartile ranges (IQR) for the baseline and the restricted viewing treatment in Microsoft Excel.

**Table 2***Ethogram Utilized for the Current Study*

Behavioral Events	Description
<i>Ear cover</i>	One or both ears are covered with palms, sides of the hands, shoulders, or substrate. Bout begins after one or both ears have been covered for two or more seconds. Bout ends immediately when both ears are uncovered. Code as ear cover when individual is laying on its side and covers opposite ear but exclude when animal is laying on its side and the opposite ear remains uncovered.
<i>Social Groom</i>	Individual picks or plucks through fur of conspecific with hands or mouth. Includes pulling out foreign items from fur and consuming them. Bout begins immediately once grooming is evident and ends as soon as social-grooming is done. If there is a five second gap between two grooming sessions, record each event separately. Focal animal may groom various body parts of conspecific as long as there is not a five second gap in between switching grooming areas.
<i>Solitary groom</i>	Individual picks or plucks through own fur with hands, feet, or mouth. Includes nose picking, scratching, lightly brushing hair with fingers and eating objects picked from fur. Focal animal may groom various body parts. Bout begins immediately once grooming is evident and ends as soon as grooming on self is done; ends five seconds after last grooming action is completed.
Behavioral States	Description
<i>Stereotypic</i>	Engages in a repetitive behavior that is not known to occur in the wild. Includes regurgitation and reingestion, and ear covering (Mason, 1991).
<i>Social play</i>	Engages in exaggerated, incomplete, non-aggressive behavior with conspecific(s). Includes wrestling, hitting, play drum, object play with another individual, grabbing, non-forceful biting, mouthing, kicking, etc.; play face (mouth is wide open with maxillary teeth visible) is often exhibited during social play.
<i>Solitary play</i>	Engages in exaggerated, incomplete, non-aggressive behavior by itself that is not directed towards another individual. Includes manipulating an object, play drum, throwing or shaking an object, hanging from a branch/vine (exclude locomotion), hand clap, etc.
<i>Social groom</i>	Picks or scratches through the fur of a conspecific with hands, feet, or mouth
<i>Solitary groom</i>	Picks through its own fur with hands, feet, or mouth; including scratching, lightly running fingers through or over fur
<i>Feeding/Foraging/Drink</i>	Consumes edible material. Includes ingesting scattered bits of food consumed while travelling, collecting food scraps, and eating large bunches of provisioned food. If an infant, nursing is included.
<i>Locomotion</i>	Moves from one location to another that is at least on body length away from its previous location (exclude movement during forage/eat, aggression, play, and stereotypic behaviors). Individual may be walking, running, or climbing in a bipedal, tripedal, or quadrupedal stance.
<i>Inactive</i>	Stationary, not engaged in play, aggression, grooming, stereotypic or feeding behaviors. Animal may be laying down on dorsal, ventral, or side of body, sitting or standing; the eyes may or may not be closed. Animal may be grasping onto a branch or arms/legs may be at a 90° angle with the body resting on substrate. Animal may switch to positions (i.e., sitting to laying down) and may look around.

*Note.* Ethogram adapted from Blaney & Wells, 2004; Clark et al., 2012; Collins & Marples, 2016; and Kuhar, 2008.

***Fecal Collection and Analysis***

**Sample Collection and Hormone Metabolite Extraction.** Fecal samples on every individual except the infant, G7, were collected three times per week throughout the study, yielding 18 samples per animal for a total of 108 samples. All samples were stored frozen in a -20 °C freezer until processing. Various colors of food dye and non-toxic glitter were used to distinguish between individuals (AmeriColor:

white, fuchsia, super black, and sky blue; Pacon: non-toxic spectra glitter, silver). Fecal samples were collected at the same time each morning to account for any diurnal cycle effects. On the day of extraction, the samples were thawed to room temperature, and  $0.50 \text{ g} \pm 0.02 \text{ g}$  of wet feces was transferred to a 16 x 125 mm polypropylene test tube.

Based on the recommendations of Palme & Möstl (1997) with slight modification, hormone metabolite extraction was achieved by adding 2.50 mL of 80% ethanol in dH<sub>2</sub>O to every test tube of weighed sample. Samples were then placed onto a rotator (Labline Maxi Rotator #4631) overnight, and the following morning, samples were centrifuged (Fisher Marathon 3000R) for 20 minutes at 2500 rpm. One milliliter of supernatant was transferred to a 12 x 75 mm polypropylene tube, securely capped to avoid evaporation, and stored at -20 °C until further analysis.

**Assay Validation and Hormone Analysis.** Commercially available enzyme immunoassays were used to quantify fecal cortisol metabolites (Arbor Assays cat # K003-H5) and fecal DHEA metabolites (Genway Biotech cat # GWB-719A7E). First, a series of biochemical validations were performed on each assay. A linearity test (parallelism) was used to determine if a serially diluted pool of a sample showed a linear decrease that ran parallel to the standard curve. This test also shows at what dilution to run samples for each assay by selecting the dilution factor of the pooled sample that is nearest 50% binding to the antibody. A recovery test (spiked standards) was also used to show the percentage recovery of exogenous hormones in the assay system. Additionally, cross-reactivity of the antibody with other analytes, assay variability using inter-and intra-coefficients of variation, and assay sensitivity were examined.

For the cortisol assay, the cross-reactivity resulted in 100.00% cortisol, 18.80% Dexamethasone, 7.80% Prednisolone, 1.20% Corticosterone, 1.20% Cortisone, and all other cross reactants were below 0.10%. Using low and high controls across all cortisol assays, the inter-assay variability produced 9.38% at 15.46% binding and 19.98% at 7.56% binding, respectively. The intra-assay coefficient of variation was 18.25% ( $n = 16$ ). Assay sensitivity was determined to be 27.60 pg/mL (standard range: 50 pg/mL-3200 pg/mL). The mean recovery of exogenous cortisol was 97.71%.

For the DHEA assay, the cross-reactivities were as follows: 100% DHEA, 4.56% Epiandrosterone, 0.61% Androstenedione, 0.50% Testosterone, 0.47% DHT, 0.42% Progesterone, and all other compounds were less than 0.30%. Also, the inter-assay variability was determined to be 10.75% at 23.13% binding and 3.37% at 10.35% binding by using low and high controls. The intra-assay coefficient of variation was 11.48% ( $n = 16$ ). The sensitivity of this assay is 0.08 ng/mL (standard range: 0.2 ng/mL-40 ng/mL). The average recovery of exogenous hormones was 88.29%.

All samples were run in duplicate and read on a Dynex Technologies MRX plate reader using Revelation software at 405 nm. Concentrations were expressed as ng/g wet feces.

## Statistical Analysis

All data were corrected for time visible to create a percentage of visible scans for behavioral states and rates for behavioral events. Behavioral diversity was calculated using the Shannon Diversity Index (Shannon, 1948), incorporating only species-specific behaviors:

$$H = - \sum_{j=1}^s p_j \ln p_j.$$

Species-specific behaviors were defined as behaviors that are observed in wild populations (Miller et al., 2020). Species-specific behavioral states included in the behavioral diversity calculations for this study were feeding/foraging/drink, locomotion, social groom, social play, and solitary groom, excluding, stereotypical behaviors. Analyses were conducted using SPSS version 22 (Chicago, IL) and Microsoft Excel. Due to non-normality of the data and small sample size, the non-parametric Wilcoxon signed rank test (Wilcoxon, 1946) was used to analyze group level differences. For all statistical tests, a value of  $p <$

.05 was utilized to determine significance. Effect sizes (Tomczak & Tomczak, 2014) for all significant results were calculated as such:

$$r = \frac{Z}{\sqrt{N}}$$

## Results

An approximate total of 119 hours of observations were completed over the course of the study, resulting in 102 10-min observation sessions per individual (G1 had 101 observation sessions). During restricted viewing, gorillas had significantly reduced solitary grooming events ( $z = -2.20, p = .03, r = .83$ ), fecal glucocorticoid metabolites ( $z = -2.20, p = .03, r = .90$ ), and the ratio of glucocorticoid metabolites to dehydroepiandrosterone metabolites ( $z = -2.20, p = .03, r = .90$ ). Considering state behaviors, restricted viewing did not impact social grooming ( $z = -0.73, p = .47$ ), solitary grooming ( $z = -0.51, p = .61$ ), solitary play ( $z = -1.75, p = .08$ ), social play ( $z = -1.75, p = .08$ ), feeding/foraging ( $z = -0.85, p = .05$ ), stereotypies ( $z = -0.73, p = .47$ ), locomotion ( $z = -0.34, p = .74$ ), or inactivity ( $z = -0.85, p = .40$ ). There were also no significant effects on the event behaviors of ear covering ( $z = -0.73, p = .47$ ) or social grooming ( $z = -0.11, p = .92$ ). Restricted viewing also had no effect on behavioral diversity ( $z = -1.35, p = .18$ ). Median, interquartile ranges, and effect sizes for behavioral and physiological data can be seen in Table 3. A visual comparison of the fecal glucocorticoid metabolites and ratio of glucocorticoid to DHEA metabolites results amid the baseline and the restricted viewing treatment is presented in Figure 2.

During the baseline condition, the median number of visitors was 2,908 and the interquartile range was 1,434. During the restricted viewing treatment, the median number of visitors was 1,931 and the interquartile range was 5,499.

**Table 3**

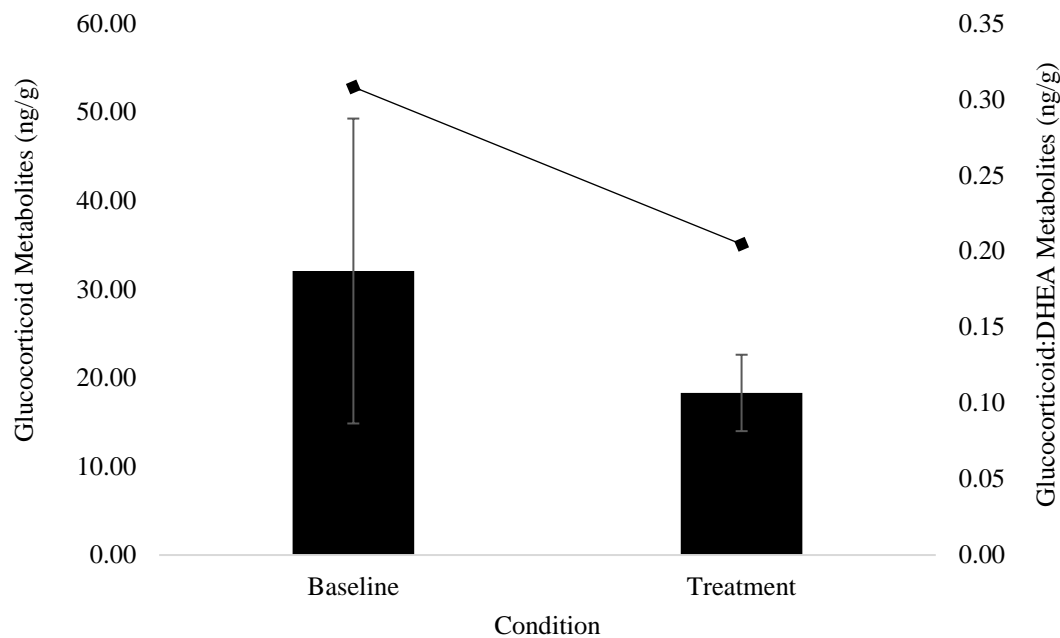
*Results for Behavioral and Physiological Data Comparing Baseline, the Restricted Viewing Treatment, and Effect Size*

Behavior	Baseline median (IQR)	Treatment median (IQR)	Effect size
Foraging	0.23 (0.11)	0.20 (0.15)	-
Inactive	0.39 (0.22)	0.39 (0.19)	-
Locomotion	0.06 (0.06)	0.04 (0.06)	-
Social Groom (State)	0.00 (0.01)	0.00 (0.01)	-
Social Play	0.00 (0.06)	0.01 (0.09)	-
Solitary Groom (State)	0.11 (0.08)	0.08 (0.08)	-
Solitary Play	0.00 (0.01)	0.01 (0.02)	-
Stereotypic	0.00 (0.02)	0.00 (0.01)	-
Behavioral Diversity	0.14 (0.24)	0.12 (0.26)	-
Ear Cover	0.00 (0.02)	0.00 (0.01)	-
Social Groom (Event)	0.01 (0.02)	0.01 (0.01)	-
Solitary Groom (Event)	0.27 (0.14)	0.18 (0.11)*	0.83
<b>Hormone</b>			
Cortisol ng/g	24.93 (11.63)	19.28 (3.52)*	0.90
Cortisol: DHEA	0.30 (0.10)	0.21 (0.05)*	0.90

*Note.* Significant results are signified with an asterisk \* $P < 0.05$ .

**Figure 2**

*Results Examining Changes in Adrenal Activity after Restricting Viewing Access.*



*Note.* Comparison between baseline and treatment for fecal glucocorticoid metabolites and ratio of glucocorticoid to DHEA metabolites.

## Discussion

The presence of visitors is inevitable in a zoological environment, so the impact of visitors is an important topic of study. This research aimed to broaden the literature by implementing an experimental design and testing multiple measures of animal welfare to examine the impact of 360° visitor viewing access on gorilla welfare. Our results suggest that the gorillas' behavior remained largely unchanged between the baseline and the restricted viewing treatment except for rates of solitary grooming. Physiologically, there was a significant reduction in the gorillas' fecal glucocorticoid metabolites and the ratio of glucocorticoid metabolites to DHEA metabolites during the restricted viewing treatment. However, there was no significant change in solitary and social play, social grooming, feeding/foraging, locomotion, stereotypies, and inactivity. Overall, restricting visitor viewing access around the gorillas' habitat resulted in a little behavior change and a reduction in hormonal measures of the adrenal system.

The incorporation of multiple measures of animal welfare in visitor effect research is essential (Clark et al., 2012; Davis et al., 2005; Peel et al., 2005; Sherwen & Hemsworth, 2019). Clark et al. (2012) conducted a study that examined the relationship between gorilla behavior, the concentration of fecal glucocorticoid (FGC) metabolites, and the zoo environment. They reported that the "negative vigilance of visitors" by the gorillas significantly increased as habitat noise did (Clark et al., 2012, p. 314). However, they concluded that the behavior change was not indicative of poor welfare since it was not associated with a significant increase in FGC levels (Clark et al., 2012). Without multiple indicators of animal welfare, Clark and colleagues (2012) would have had less support for this claim. Alternatively, we observed a significant reduction in the gorillas' physiology and solitary grooming rates in response to restricted visitor viewing. Thus, decreasing visitor viewing access may be beneficial to zoo-housed gorillas. However, the results of the current study should be interpreted with caution. Since animal welfare is the utmost priority in zoos, research is limited by what can and cannot be controlled, even with an experimental design. Confounds are likely and may have contributed to the effects seen here. For instance, the barriers restricted



visitor viewing access but could have also reduced visitor presence, viewing time by guests, noise levels, and increased available hiding spaces for the gorillas. Regardless, physical barriers are still an opportunity for future visitor effect research. In general, our results support the notion of other scientists that no single metric is an optimal measure of animal welfare. Striving for a holistic approach by incorporating multiple measures is crucial.

A few studies on solitary grooming have demonstrated that increased self-scratching and auto grooming rates can be linked with stressful situations and increase physiological stress (Castles et al., 1999; Clark et al., 2012; Leeds & Lukas, 2018; Maestriperi et al., 1992; Schino et al., 2007). However, extensive research examining grooming behavior broadly in primates and gorillas notes a significant relationship between grooming and social hierarchy (Huskinson & Chism, 2018; Robbins et al., 2005; Watts, 1994). It is difficult to discern whether the behavior results seen here are stress-related or socially influenced given the limited research comparing gorilla solitary grooming to other behaviors, physiology, and the presence of visitors. Future research exploring how visitors impact solitary grooming rates and its relation to gorilla welfare is necessary. An investigation of the impact of visitor presence that accounts for a range of behaviors paired with physiological measures across multiple institutions, as well as evaluating space use, would provide deeper insight into the results from the current study.

Visitor noise levels, crowd size, and crowd activity are associated with immediate and longitudinal behavior change in zoo animals (Birke, 2002; Hosey, 2008; Kuhar, 2008; Mitchell et al., 1992; Morgan & Tromborg, 2007; Quadros et al., 2014; Sherwen & Hemsworth, 2019; Wood, 1998). During the study (September-November 2019), there was a steady decline in visitor numbers. The median number of guests during the baseline was higher than during the restricted viewing treatment. The decline in guests could have resulted in decreased noise levels, crowd size, or crowd activity, which may have reduced solitary grooming rates and hormone levels in the gorillas. However, the higher interquartile range during the restricted viewing treatment shows there was more crowd variability during this time. Although the varying guest count between the conditions makes it difficult to tease apart which visitor variable influenced the results seen here, our immediate interest was to assess 360° visitor viewing access. We were interested in how the mere presence of visitors and their positioning around the exhibit influenced the gorillas' behavior and physiology rather than the total number of guests. Furthermore, the methodology of a study is critical to consider; in the future, it would be valuable to replicate this study using an ABAB design rather than AB design, as seen here to better control for potential confounds. In addition to an ABAB design, it may be beneficial to perform reversals of the study, which parallels Chiew and colleagues' (2020) research. Extending the observational period over the busier months of the year, increasing the sample size, and incorporating multiple visitor variables, including continuous recording of crowd size and decibel levels, would allow for a more robust analysis.

While there were some significant changes observed, the majority of gorilla behavior was consistent between conditions. The gorillas' rates of play and stereotypic behavior remained unchanged when comparing the baseline to the restricted viewing treatment. Both behaviors are indicators of animal welfare (Ahloy-Dallaire et al., 2018; Held & Špinká, 2011; Mason, 1991). The prevalence of stereotypic behavior can be a sign of suboptimal environments and is generally considered a negative indicator of welfare (Mason, 1991; Veasey et al., 1996). In contrast, play behavior and behavioral diversity are generally recognized as positive indicators of welfare (Burghardt, 2005; Carrasco et al., 2009; Held & Špinká, 2011; Miller et al., 2020; Oliveira et al., 2010). The individuality of the gorillas and their complex social nature may be one explanation for the consistency in behavior across conditions (Carder & Semple, 2008; Collins & Marples, 2016; Maestriperi & Ross, 2004; Polgár et al., 2017; Stoinski et al., 2012; Woods et al., 2019). Alternatively, it could be that restricting access of viewing does not impact gorilla welfare. Delving deeper into assessments of welfare is essential going forward to have a better understanding of restricting visitor viewing access.

Our study sought to contribute a unique perspective to the visitor effect literature by implementing an experimental design that utilized both behavior and physiology measures and examining a factor that, to our knowledge, has not yet been investigated in primates (360° visitor viewing access). We found a significant decrease in solitary grooming bouts, fecal glucocorticoid metabolites, and the ratio of

glucocorticoid metabolites to dehydroepiandrosterone (DHEA) metabolites following restricted viewing access. However, there was no significant change in multiple behaviors that have been used as welfare indicators in previous research, leaving an unclear picture of how restricted visitor viewing affected the gorillas' welfare. Overall, our findings emphasize the importance of incorporating multiple measures when examining the effects of visitors on animal welfare. The results of our novel experiment may help guide future research in this field and inform ongoing habitat design decisions for gorillas and other species.

### Conclusions

1. The Western lowland gorillas had a significant reduction in solitary grooming and two hormonal measures of the adrenal system when comparing baseline to treatment.
2. The majority of behaviors observed during the study remained consistent across conditions for this group of gorillas.
3. Future research is necessary to better understand the impact of restricted viewing on the welfare of gorillas in a zoological setting.

### Acknowledgements

Thank you to the Chicago Zoological Society's Tropic World animal care staff for their help and assistance making this project possible. The authors would also like to thank John Anglin for assisting with the development of this project as well as data collection. We also thank Sarah Breen-Barteccki and Bill Zeigler for their continued support.

### References

- Ahloy-Dallaire, J., Espinosa, J., & Mason, G. (2018). Play and optimal welfare: Does play indicate the presence of positive affective states? *Behavioural Processes*, *156*, 3–15. <https://doi.org/10.1016/j.beproc.2017.11.011>
- Birke, L. (2002). Effects of browse, human visitors and noise on the behaviour of captive orangutans. *Animal Welfare*, *11*, 189–202.
- Bitgood, S., Patterson, D., & Benefield, A. (1988). Exhibit design and visitor behavior: Empirical relationships. *Environment and Behavior*, *20*(4), 474–491. <https://doi.org/10.1177/0013916588204006>
- Blaney, E. C., & Wells, D. L. (2004). The influence of a camouflage net barrier on the behaviour, welfare and public perceptions of zoo-housed gorillas. *Animal Welfare*, *13*(2), 111–118.
- 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. <https://doi.org/10.1002/zoo.21207>
- Bonnie, K. E., Ang, M. Y., & Ross, S. R. (2016). Effects of crowd size on exhibit use by and behavior of chimpanzees (*Pan troglodytes*) and Western lowland gorillas (*Gorilla gorilla*) at a zoo. *Applied Animal Behaviour Science*, *178*, 102–110. <https://doi.org/10.1016/j.applanim.2016.03.003>
- Brand, C. M., Boose, K. J., Squires, E. C., Marchant, L. F., White, F. J., Meinelt, A., & Snodgrass, J. J. (2016). Hair plucking, stress, and urinary cortisol among captive bonobos (*Pan paniscus*). *Zoo Biology*, *35*(5), 415–422. <https://doi.org/10.1002/zoo.21320>
- Broom, D. M., & Johnson, K. G. (1993). *Stress and animal welfare: Key issues in the biology of humans and other animals* (2<sup>nd</sup> ed.). Chapman & Hall. <https://doi.org/10.1007/978-3-030-32153-6>
- Burghardt, G. M. (2005). *The genesis of animal play: Testing the limits*. MIT Press.
- 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. <https://doi.org/10.1016/j.applanim.2008.06.001>
- Carlstead, K., & Brown, J. L. (2005). Relationships between patterns of fecal corticoid excretion and behavior, reproduction, and environmental factors in captive black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros. *Zoo Biology*, *24*(3), 215–232. <https://doi.org/10.1002/zoo.20050>
- Carlstead, K., Fraser, J., Bennett, C., & Kleiman, D. G. (1999). Black rhinoceros (*Diceros bicornis*) in US zoos: II. Behavior, breeding success, and mortality in relation to housing facilities. *Zoo Biology*, *18*(1), 35–52. [https://doi.org/10.1002/\(SICI\)1098-2361\(1999\)18:1<35::AID-ZOO5>3.0.CO;2-L](https://doi.org/10.1002/(SICI)1098-2361(1999)18:1<35::AID-ZOO5>3.0.CO;2-L)
- Carrasco, L., Colell, M., Calvo, M., Abello, M. T., Velasco, M., & Posada, S. (2009). Benefits of training/playing therapy in a group of captive lowland gorillas (*Gorilla gorilla gorilla*). *Animal Welfare*, *18*(1), 9–19.

- Castles, D. L., Whiten, A., & Aureli, F. (1999). Social anxiety, relationships and self-directed behaviour among wild female olive baboons. *Animal Behaviour*, 58(6), 1207–1215. <https://doi.org/10.1006/anbe.1999.1250>
- Chamove, A. S., Hosey, G. R., & Schaetzel, P. (1988). Visitors excite primates in zoos. *Zoo Biology*, 7(4), 359–369. <https://doi.org/10.1002/zoo.1430070407>
- Chiew, S. J., Butler, K. L., Sherwen, S. L., Coleman, G. J., Fanson, K. V., & Hemsworth, P. H. (2019). Effects of regulating visitor viewing proximity and the intensity of visitor behaviour on little penguin (*Eudyptula minor*) behaviour and welfare. *Animals*, 9(6), 285. <https://doi.org/10.3390/ani9060285>
- Chiew, S. J., Butler, K. L., Sherwen, S. L., Coleman, G. J., Melfi, V., Burns, A., & Hemsworth, P. H. (2020). Effect of covering a visitor viewing area window on the behaviour of zoo-housed little penguins (*Eudyptula minor*). *Animals*, 10(7), 1224. <https://doi.org/10.3390/ani10071224>
- Choo, Y., Todd, P. A., & Li, D. (2011). Visitor effects on zoo orangutans in two novel, naturalistic enclosures. *Applied Animal Behaviour Science*, 133(1–2), 78–86. <https://doi.org/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. (2012). Relationship between behavior, adrenal activity, and environment in zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biology*, 31(3), 306–321. <https://doi.org/10.1002/zoo.20396>
- 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. <https://doi.org/10.1002/zoo.21370>
- 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), 183–192. <https://doi.org/10.1111/izy.12111>
- Cooke, C. M., & Schillaci, M. A. (2007). Behavioral responses to the zoo environment by white handed gibbons. *Applied Animal Behaviour Science*, 106(1-3), 125–133. <https://doi.org/10.1016/j.applanim.2006.06.016>
- Davey, G. (2007). Visitors' effects on the welfare of animals in the zoo: A review. *Journal of Applied Animal Welfare Science*, 10(2), 169–183. <https://doi.org/10.1080/10888700701313595>
- Davis, N., Schaffner, C. M., & Smith, T. E. (2005). Evidence that zoo visitors influence HPA activity in spider monkeys (*Ateles geoffroyi rufiventris*). *Applied Animal Behaviour Science*, 90(2), 131–141. <https://doi.org/10.1016/j.applanim.2004.08.020>
- Fernandez, 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. <https://doi.org/10.1016/j.applanim.2009.06.002>
- Goodenough, A. E., McDonald, K., Moody, K., & Wheeler, C. (2019). Are "visitor effects" overestimated? Behaviour in captive lemurs is mainly driven by co-variation with time and weather. *Journal of Zoo and Aquarium Research*, 7(2), 59–66. <https://doi.org/10.19227/jzar.v7i2.343>
- Hansen, B. K., Hopper, L. M., Fultz, A. L., & Ross, S. R. (2020). Understanding the behavior of sanctuary-housed chimpanzees during public programs. *Anthrozoös*, 33(4), 481–495. <https://doi.org/10.1080/08927936.2020.1771055>
- Hashmi, A., & Sullivan, M. (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), 268–282. <https://doi.org/10.19227/jzar.v8i4.523>
- Held, S. D., & Špinka, M. (2011). Animal play and animal welfare. *Animal Behaviour*, 81(5), 891–899. <https://doi.org/10.1016/j.anbehav.2011.01.007>
- Hosey, G. R. (2000). Zoo animals and their human audiences: What is the visitor effect? *Animal Welfare*, 9(4), 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. <https://doi.org/10.1016/j.applanim.2004.08.015>
- Hosey, G. (2008). A preliminary model of human–animal relationships in the zoo. *Applied Animal Behaviour Science*, 109(2–4), 105–127. <https://doi.org/10.1016/j.applanim.2007.04.013>
- 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. [https://doi.org/10.1016/0168-1591\(87\)90251-6](https://doi.org/10.1016/0168-1591(87)90251-6)
- Hosey, G., Melfi, V., Formella, I., Ward, S. J., Tokarski, M., Brunger, D., Brice, S. & Hill, S. P. (2016). Is wounding aggression in zoo-housed chimpanzees and ring-tailed lemurs related to zoo visitor numbers? *Zoo Biology*, 35, 205–209. <https://doi.org/10.1002/zoo.21277>
- Huskinson, S. M., & Chism, J. L. (2018). Emerging relationships in a new group of Western lowland gorillas *Gorilla gorilla gorilla* at Riverbanks Zoo & Garden, Columbia, SC. *International Zoo Yearbook*, 52(1), 92–102. <https://doi.org/10.1111/izy.12183>

- Kamin, H. S., & Kertes, D. A. (2017). Cortisol and DHEA in development and psychopathology. *Hormones and Behavior*, 89, 69–85. <https://doi.org/10.1016/j.yhbeh.2016.11.018>
- Kuhar, C. W. (2008). Group differences in captive gorillas' reaction to large crowds. *Applied Animal Behaviour Science*, 110(3-4), 377–385. <https://doi.org/10.1016/j.applanim.2007.04.011>
- Landis, J. R., & Koch, G. G. (1977). The measurement of observer agreement for categorical data. *Biometrics*, 30(1), 159–174.
- Leeds, A., & Lukas, K. E. (2018). Experimentally evaluating the function of self-directed behaviour in two adult mandrills (*Mandrillus sphinx*). *Animal Welfare*, 27(1), 81–86. <https://doi.org/10.7120/09627286.27.1.081>
- Lewis, R. N., Chang, Y. M., Ferguson, A., Lee, T., Clifford, L., & Abeyesinghe, S. M. (2020). The effect of visitors on the behavior of zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biology*, 39(5), 283–296. <https://doi.org/10.1002/zoo.21552>
- Maestriperi, D., & Ross, S. R. (2004). Sex differences in play among western lowland gorilla (*Gorilla gorilla gorilla*) infants: Implications for adult behavior and social structure. *American Journal of Physical Anthropology*, 123(1), 52–61. <https://doi.org/10.1002/ajpa.10295>
- Maestriperi, D., Schino, G., Aureli, F., & Troisi, A. (1992). A modest proposal: Displacement activities as an indicator of emotions in primates. *Animal Behaviour*, 44(5), 967–979. [https://doi.org/10.1016/S0003-3472\(05\)80592-5](https://doi.org/10.1016/S0003-3472(05)80592-5)
- Martín, O., Vinyoles, D., García-Galea, E., & Maté, C. (2016). Improving the welfare of a zoo-housed male drill (*Mandrillus leucophaeus poensis*) aggressive towards visitors. *Journal of Applied Animal Welfare Science*, 19(4), 323–334. <https://doi.org/10.1080/10888705.2016.1147961>
- Mason, G. J. (1991). Stereotypies: A critical review. *Animal Behaviour*, 41(6), 1015–1037. [https://doi.org/10.1016/S0003-3472\(05\)80640-2](https://doi.org/10.1016/S0003-3472(05)80640-2)
- Miller, L. J., Ivy, J. A., Vicino, G. A., & Schork, I. G. (2019). Impacts of natural history and exhibit factors on carnivore welfare. *Journal of Applied Animal Welfare Science*, 22(2), 188–196. <https://doi.org/10.1080/10888705.2018.1455582>
- Miller, L. J., Vicino, G. A., Sheftel, J., & Lauderdale, L. K. (2020). Behavioral diversity as a potential indicator of positive animal welfare. *Animals*, 10(7), 1211. <https://doi.org/10.3390/ani10071211>
- Mitchell, G., Tromborg, C. T., Kaufman, J., Bargabus, S., Simoni, R., & Geissler, V. (1992). More on the 'influence' of zoo visitors on the behaviour of captive primates. *Applied Animal Behaviour Science*, 35(2), 189–198. [https://doi.org/10.1016/0168-1591\(92\)90009-Z](https://doi.org/10.1016/0168-1591(92)90009-Z)
- Morgan, K. N., & Tromborg, C. T. (2007). Sources of stress in captivity. *Applied Animal Behaviour Science*, 102(3–4), 262–302. <https://doi.org/10.1016/j.applanim.2006.05.032>
- Möstl, E., & Palme, R. (2002). Hormones as indicators of stress. *Domestic Animal Endocrinology*, 23(1–2), 67–74. [https://doi.org/10.1016/S0739-7240\(02\)00146-7](https://doi.org/10.1016/S0739-7240(02)00146-7)
- Nimon, A. J., & Dalziel, F. R. (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(2–3), 261–272. [https://doi.org/10.1016/S0168-1591\(05\)80013-9](https://doi.org/10.1016/S0168-1591(05)80013-9)
- Oliveira, A. F. S., Rossi, A. O., Silva, L. F. R., Lau, M. C., & Barreto, R. E. (2010). Play behaviour in nonhuman animals and the animal welfare issue. *Journal of Ethology*, 28(1), 1–5. <https://doi.org/10.1007/s10164-009-0167-7>
- Palme, R. (2019). Non-invasive measurement of glucocorticoids: Advances and problems. *Physiology & Behavior*, 199, 229–243. <https://doi.org/10.1016/j.physbeh.2018.11.021>
- Palme, R., & Möstl, E. (1997). Measurement of cortisol metabolites in faeces of sheep as a parameter of cortisol concentration in blood. *Zeitschrift Fuer Saeugetierkunde*, 62(2), 192–197.
- Peel, A. J., Vogelnest, L., Finnigan, M., Grossfeldt, L., & O'Brien, J. K. (2005). Non-invasive fecal hormone analysis and behavioral observations for monitoring stress responses in captive Western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biology*, 24(5), 431–445. <https://doi.org/10.1002/zoo.20055>
- Polgár, Z., Wood, L., & Haskell, M. J. (2017). Individual differences in zoo-housed squirrel monkeys' (*Saimiri sciureus*) reactions to visitors, research participation, and personality ratings. *American Journal of Primatology*, 79(5), e22639. <https://doi.org/10.1002/ajp.22639>
- Quadros, S., Goulart, V. D., Passos, L., Vecci, M. A., & Young, R. J. (2014). Zoo visitor effect on mammal behaviour: Does noise matter?. *Applied Animal Behaviour Science*, 156, 78–84. <https://doi.org/10.1016/j.applanim.2014.04.002>

- Robbins, M. M., Gerald-Steklis, N., Robbins, A. M., & Steklis, H. D. (2005). Long-term dominance relationships in female mountain gorillas: Strength, stability and determinants of rank. *Behaviour*, *142*(6), 779–809. <https://doi.org/10.1163/1568539054729123>
- Schino, G., di Sorrentino, E. P., & Tiddi, B. (2007). Grooming and coalitions in Japanese macaques (*Macaca fuscata*): Partner choice and the time frame reciprocation. *Journal of Comparative Psychology*, *121*(2), 181. <https://doi.org/10.1037/0735-7036.121.2.181>
- Shannon, C. E. (1948). A mathematical theory of communication. *The Bell System Technical Journal*, *27*(3), 379–423. <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>
- Sherwen, S. L., & Hemsworth, P. H. (2019). The visitor effect on zoo animals: Implications and opportunities for zoo animal welfare. *Animals*, *9*(6), 366. <https://doi.org/10.3390/ani9060366>
- 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. <https://doi.org/10.1016/j.applanim.2015.03.004>
- Sherwen, S. L., Magrath, M. J., Butler, K. L., & Hemsworth, P. H. (2015). Little penguins, *Eudyptula minor*, show increased avoidance, aggression and vigilance in response to zoo visitors. *Applied Animal Behaviour Science*, *168*, 71–76. <https://doi.org/10.1016/j.applanim.2015.04.007>
- Shweta, Bajpai, R. C., & Chaturvedi, H. K. (2015). Evaluation of inter-rater agreement and inter-rater reliability for observational data: An overview of concepts and methods. *Journal of the Indian Academy of Applied Psychology*, *41*(3), 20–27.
- 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), 586–599. <https://doi.org/10.1002/zoo.20425>
- Todd, P. A., Macdonald, C., & Coleman, D. (2007). Visitor-associated variation in captive Diana monkey (*Cercopithecus diana diana*) behaviour. *Applied Animal Behaviour Science*, *107*(1–2), 162–165. <https://doi.org/10.1016/j.applanim.2006.09.010>
- Tomczak, M., & Tomczak, E. (2014). The need to report effect size estimates revisited. An overview of some recommended measures of effect size. *Trends in Sport Sciences*, *21*(1), 19–25.
- Touma, C., & Palme, R. (2005). Measuring fecal glucocorticoid metabolites in mammals and birds: The importance of validation. *Annals of the New York Academy of Sciences*, *1046*(1), 54–74. <https://doi.org/10.1196/annals.1343.006>
- 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. *Animal Welfare*, *5*, 13–24.
- Wark, J. D., Cronin, K. A., Niemann, T., Shender, M. A., Horrigan, A., Kao, A., & Ross, M. R. (2019). Monitoring the behavior and habitat use of animals to enhance welfare using the ZooMonitor app. *Animal Behavior and Cognition*, *6*(3), 158–167. <https://doi.org/10.26451/abc.06.03.01.2019>
- Watts, D. P. (1994). Agonistic relationships between female mountain gorillas (*Gorilla gorilla beringei*). *Behavioral Ecology and Sociobiology*, *34*(5), 347–358. <https://doi.org/10.1007/BF00197005>
- Whitham, J. C., Bryant, J. L., & Miller, L. J. (2020). Beyond glucocorticoids: Integrating dehydroepiandrosterone (DHEA) into animal welfare research. *Animals*, *10*(8), 1381. <https://doi.org/10.3390/ani10081381>
- Whitham, J. C., & Wielebnowski, N. (2013). New directions for zoo animal welfare science. *Applied Animal Behaviour Science*, *147*(3–4), 247–260. <https://doi.org/10.1016/j.applanim.2013.02.004>
- Wielebnowski, N., & Watters, J. (2007). Applying fecal endocrine monitoring to conservation and behavior studies of wild mammals: Important considerations and preliminary tests. *Israel Journal of Ecology and Evolution*, *53*(3–4), 439–460. <https://doi.org/10.1560/IJEE.53.3.439>
- Wilcoxon, F. (1946). Individual comparisons of grouped data by ranking methods. *Journal of Economic Entomology*, *39*(2), 269–270. <https://doi.org/10.1093/jee/39.2.269>
- Wood, W. (1998). Interactions among environmental enrichment, viewing crowds, and zoo chimpanzees (*Pan troglodytes*). *Zoo Biology*, *17*(3), 211–230. [https://doi.org/10.1002/\(SICI\)1098-2361\(1998\)17:3<211::AID-ZOO5>3.0.CO;2-C](https://doi.org/10.1002/(SICI)1098-2361(1998)17:3<211::AID-ZOO5>3.0.CO;2-C)
- Woods, J. M., Ross, S. R., & Cronin, K. A. (2019). The social rank of zoo-housed Japanese Macaques is a predictor of visitor-directed aggression. *Animals*, *29*(6), 316. <https://doi.org/10.3390/ani9060316>