Journal of
Zoological and Botanical Gardens

MDPI

Article

Comparing Space Use and Fecal Glucocorticoid Concentrations during and after the COVID-19 Closure to Investigate Visitor Effects in Multiple Species

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Abstract: We used the COVID-19 pandemic closure at the Saint Louis Zoo to examine visitor effects on space use and glucocorticoid levels in banteng, grizzly bears, polar bears, and western lowland gorillas. The study was divided into four six-week phases: closure in spring 2020, reopening in summer 2020, fall 2020, and spring 2021 as a seasonal comparison. Space use data were collected using video, and fecal samples were assayed for glucocorticoids. Generalized linear models were used to examine differences in zone occupancy and glucocorticoids between phases. The banteng spent more time near visitors, and glucocorticoids were only temporarily elevated in two of five animals when visitors returned. The grizzly bears spent more time in their habitat than in the den, and the polar bear spent more time near viewing areas after visitors returned. Glucocorticoids did not differ significantly between the closure and reopening for any bears. The gorillas spent less time close to visitors immediately after reopening but this effect waned by fall; glucocorticoid data were not available. Overall, based on space use and glucocorticoid levels, we suggest visitor effects on the gorillas are neutral, on the grizzly bears are neutral or positive, and are positive on the banteng and polar bear.

Keywords: physiology; cortisol; zoo research; behavior; banteng; gorillas; grizzly bears; polar bears

Citation: Edes, A.N.; Liu, N.C.; Baskir, E.; Bauman, K.L.; Kozlowski, C.P.; Clawitter, H.L.; Powell, D.M. Comparing Space Use and Fecal Glucocorticoid Concentrations during and after the COVID-19 Closure to Investigate Visitor Effects in Multiple Species. *J. Zool. Bot. Gard.* **2022**, *3*, 328–348. https://doi.org/10.3390/jzbg3030026

Academic Editor: Steven Monfort

Received: 3 May 2022
Accepted: 27 June 2022
Published: 5 July 2022

1. Introduction

The effect of visitors on zoo-housed animals is frequently characterized as positive, negative, or neutral based on the behavioral or physiological responses of various species. For example, Mexican wolves (*Canis lupus baileyi*) spent less time resting and eating and had higher fecal glucocorticoid levels on days with larger crowds [1], suggesting a negative visitor effect. In contrast, behavioral diversity in Gentoo penguins (*Pygoscelis papua*) was associated with higher visitor counts [2], indicating a positive or stimulating effect. To lesser anteaters (*Tamandua tetradactyla*), visitors may be a neutral stimulus, as they showed no differences in behavior, the timing of activity, or space use when visitors were present or absent [3]. Although visitor effects are frequently studied in zoos, substantial inter- and intra-specific variation in responses have made it difficult to draw definitive conclusions about the effect of visitors, even within a single species. For example, one study reported no significant effect of crowd size on pacing by jaguars (*Panthera onca*) [4], while another reported a positive association [5]. For a recent comprehensive review of visitor effect research in zoos, see [6].

Visitors present a wide array of stimuli, including visual, auditory, and olfactory. As it is often difficult to distinguish between these stimuli and determine the exact cause of

changes in behavior and/or physiology, many studies focus instead on whether visitors are present or absent [7–9]. One challenge in these studies is that times without visitors in a zoo are infrequent. As such, zoo closures in early 2020 as a result of the COVID-19 pandemic provided a unique opportunity to study visitor effects without this limitation. Importantly, to minimize the disruption to the animals in their care, many zoos worked to maintain normal husbandry and management routines during the closures.

Several published studies have already compared behavioral and physiological data collected during COVID-19 closures with data collected prior to the closure or after reopening. As seen in other visitor effects studies, a mixture of positive, negative, and neutral effects was reported. Nile crocodiles (*Crocodylus niloticus*) spent more time in proximity to conspecifics when the zoo was open compared to closed [10], and Japanese macaques (*Macaca fuscata*) seemed to prefer completing trials in testing booths closest to the public when the zoo reopened [11]. Five primate species, including Eastern black-and-white colobus (*Colobus guereza*), Allen's swamp monkeys (*Allenopithecus nigroviridis*), DeBrazza's monkeys (*Cercopithecus neglectus*), Bolivian gray titi monkeys (*Callicebus donacophilus*), and crowned lemurs (*Eulemur coronatus*), showed a slight but significant increase in proximity to the glass when open versus closed [12]. Catalina Island rattlesnakes (*Crotalus catalinensis*) showed more social and investigative behaviors after reopening [13]. Beaded lizards (*Heloderma horridum exasperatum*) [14] and multiple bear species, including Andean (*Tremarctos ornatus*), sloth (*Melursus ursinus*), sun (*Helarctos malayanus*), grizzly (*Ursus arctos horribilis*), and black bears (*Ursus americanus*), were more visible when visitors were present [15], suggesting a positive effect of visitors. On the other hand, European glass lizards (*Pseudopus apodus*) [13], meerkats (*Suricata suricatta*) [16], African penguins (*Spheniscus demersus*) [16], and red kangaroos (*Macropus rufus*) [17] used more of their enclosure when the zoo was closed, Chilean flamingos (*Phoenicopterus chilensis*) decreased activity and feeding when the zoo reopened (although the authors indicate these changes may be more due to weather) [18], and European glass lizards [13], Chinese crocodile lizards (*Shinisaurus crocodilurus*), and tokay geckos (*Gekko gecko*) [14] were less visible under open conditions.

Overall, however, most studies conducted during COVID-19 closures reported entirely or mainly neutral effects that suggest a minimal impact from visitors. There were no significant differences in behavior between the closures and open periods reported for western lowland gorillas (*Gorilla gorilla gorilla*) [19], African penguins [16], greater flamingos (*Phoenicopterus roseus*) [18], Amur leopards (*Panthera pardus orientalis*), snow leopards (*Panthera uncia*), Rothschild giraffes (*Giraffa camelopardalis*), Chapman's zebras (*Equus quagga chapmani*), nyala (*Tragelaphus angasii*), swamp wallabies (*Wallabia bicolor*) [20], Eastern black-and-white colobus, Allen's swamp monkeys, DeBrazza's monkeys, Bolivian gray titi monkeys, or crowned lemurs [12]. Additionally, Nile crocodiles [10], greater and Chilean flamingos [18], Amur leopards, snow leopards, Rothschild giraffes, Chapman's zebras, nyala, swamp wallabies, and Chinese gorals (*Naemorhedus griseus*) [20] showed no difference in space use between open and closed periods. There also were minimal differences in levels of behavior, space use, and/or visibility in multiple species of reptiles [13,14]. Similarly, while visibility initially declined with the return of visitors for several amphibian species, that effect waned with time, and visibility returned to or increased above closure levels [21]. In Japanese macaques, there was no difference between the closure and reopening on the number of cognitive trials animals chose to participate in, the number of trials they completed per session, or their accuracy on the tasks [11]. Physiologically, neither cheetahs (*Acinonyx jubatus*) nor giraffes (*G. c. reticulata*, *G. tippelskirchi*) showed significant differences in fecal glucocorticoid levels between matched open and closed periods [22].

Many COVID-19 closure studies also showed variation in visitor effects on a single species, either within the same group or between groups at different locations. For example, although not significant, the silverback male in a gorilla troop increased his foraging time and decreased his inactivity during the closure, while the other five members of his group decreased foraging and increased inactivity [19]. Nile crocodiles showed more agonism but also more conspecific bunting, a positive social behavior, during the closure [10].

Meerkats behaved differently across three zoos, with some groups showing increases in environmental interaction, positive social interaction, or vigilance during the closure, while other groups did not [16].

Our objective was to use the COVID-19 closure to gain insight into how visitors impact space use and physiology in four species housed at the Saint Louis Zoo, including banteng (*Bos javanicus*), grizzly bears, polar bears (*U. maritimus*), and western lowland gorillas. Increased time spent in proximity to viewing areas when guests returned was interpreted to indicate a positive effect of visitors and vice versa. A similar approach has been used in other studies. Gorillas and chimpanzees (*Pan troglodytes*) did not vary their use of a zone within 1m of the viewing glass based on crowd size [23]. Eastern black-and-white colobus, Allen's swamp monkeys, DeBrazza's monkeys, Bolivian gray titi monkeys, and crowned lemurs showed an increase in proximity to viewing windows, both with larger crowd sizes and when the zoo was open than during the COVID-19 closure [12]. Other COVID-19 studies also examined proximity to guests as an indicator of visitor effects. For example, Grevy's zebra spent more time in spaces close to public viewing areas than expected by chance when the zoo was closed and less time than expected by chance when the zoo was open [20]. Additionally, Chilean flamingos used a hill zone near visitor viewing areas more frequently after reopening [18], and meerkats at one zoo spent more time in the area closest to visitors while meerkats at two other zoos spent more time in the area furthest from visitors after reopening [16].

As an indicator of hypothalamic-pituitary-adrenal (HPA) axis activity, glucocorticoid levels can provide information on levels of arousal experienced by an individual, with higher levels generally indicating increased arousal, either positive or negative [24,25]. Fecal glucocorticoids are commonly used to investigate how animals respond to environmental changes and events from a physiological perspective and, as such, have been incorporated into visitor effect research. For example, clouded leopards (*Neofelis nebulosa*) on display had higher fecal glucocorticoids than those not on display [26], black-capped capuchins (*Cebus apella*) had lower glucocorticoids on average when one-way viewing screens were in place [27], and meerkats showed a positive association between crowd size and fecal glucocorticoids [28]. On the other hand, there were no significant correlations between visitor numbers and glucocorticoids in African penguins [29] or kangaroos (*Macropus fuliginosus*) and red kangaroos [30], and fecal glucocorticoids in gorillas did not vary based on crowd size, noise levels, or frequency of camera flashes [31]. While glucocorticoids can provide insight into how animals perceive experiences, there are also limitations to their use, especially as increases are frequently interpreted as evidence of stress. Glucocorticoids play functions outside of stress responses, such as the awakening response and energy metabolism [24,32], and fluctuations can be associated with season, breeding, or a variety of factors other than stress [33–35]. Glucocorticoid responses also have been shown to vary widely between individuals and even within the same individual at different points in time [33–39]. As such, it is critical to keep in mind that an increase in glucocorticoid levels is not synonymous with a negative experience or perspective, or with "stress" [24,25,40,41].

In this study, we compared the spring 2020 COVID-19 closure with three additional periods, including immediately following reopening in summer 2020, in fall 2020 after a period of potential re-acclimation to guests, and a time-matched period in spring 2021. The comparison one year following the closure was critical to determine if any changes observed were likely due to season rather than visitor presence, as some animals can show seasonal variation in both behavior and physiology. Recent research investigating visitor effects in ring-tailed lemurs (*Lemur catta*) [42], hornbills (*Ceratogymna atrata*) [43], and flamingos [18] has shown that observed changes in behavior and/or physiology were primarily explained by variables such as time, temperature, and weather rather than guests. Because these variables are correlated with visitor number, both accounting for and disentangling them from visitor effects is critical but difficult. Some of the previously published research on COVID-19 closures controlled for seasonal variation as well, such as by comparing the