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# ‘Bearly’ Changing with the Seasons: Bears of Five Species Show Few Behavioral Changes Across Seasons and at Varying Visitor Densities

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**Abstract** – In natural environments, bear behavior follows seasonal patterns but the zoo environment differs from the natural environment in several ways, including the presence of zoo visitors. Although typically difficult to disentangle, we were able to tease apart the effects of seasonal changes and visitor density on the visibility and behavior of 10 bears representing five species housed at Cleveland Metroparks Zoo due to the disruption caused by COVID-19. We conducted a longitudinal bear behavior monitoring project from June, 2017-November, 2020. Bears were more visible in the spring and in the presence of visitors, locomoted more and were less inactive when large crowds were present, foraged and locomoted more when it was earlier in the day, and locomoted more at higher temperatures. There were limited differences in bear visibility to observers between 2020 (when the zoo was temporarily closed to visitors) and the previous three years. There were no differences in rates of stereotypy or social behavior across seasons, crowds, or daily attendance categories. Based on these limited differences, neither season nor visitor density seemed to have an apparent effect on bear behavior or welfare.

**Keywords** – Visitor effect, Daily attendance, Crowd size, Bear behavior, COVID-19, Season

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Bear behavioral ecology is influenced by seasonal changes in natural environmental factors such as daylight, temperature, and food availability (Stirling & Derocher, 1990). When caring for bears, these factors are taken into account by zoo managers, along with other environmental variables over which they have control, such as habitat size and features, ambient noise, caretaker interactions, and proximity to and protection from visitors. How these natural and zoo environmental variables affect bear behavior and welfare is of great interest to zoo managers, but the effects of these variables can be difficult to disentangle. In particular, the effects of season and visitor density are typically confounded as zoos tend to experience an increase in visitor numbers during warm weather (Perkins & Debbage, 2016). Due to the spread of the coronavirus, COVID-19, Cleveland Metroparks Zoo closed for three months during the spring of 2020. This unexpected and temporary zoo closure allowed us to address this question by comparing seasonal effects on bear behavior across a four-year period, including 2020.

For all species of bear, diets vary seasonally, depending on the part of the world they inhabit (sloth bears (*Melursus ursinus*), Joshi et al., 1997, Mewada & Dharaiya, 2010; Andean bears

(*Tremarctos ornatus*), García-Rangel, 2012; brown bears (*Ursus arctos*), Mowat & Heard, 2006; Munro et al., 2006; American black bears (*Ursus americanus*), Lesmerises et al., 2015; Mosnier et al., 2008; polar bears (*Ursus maritimus*), Galicia et al., 2015; Asiatic black bears (*Ursus thibetanus*), Ali et al., 2017; sun bears (*Helarctos malayanus*), Fredriksson et al., 2006; giant pandas (*Ailuropoda melanoleuca*), Cabana et al., 2020; Li et al., 2017). Home ranges vary as well, as bears migrate to find available food (sloth bears, Joshi et al., 1997; Andean bears, García-Rangel, 2012; brown bears, Mowat & Heard, 2006; Munro et al., 2006; American black bears, Bonin et al., 2020; polar bears, Ferguson et al., 1999; Asiatic black bears, Izumiyama & Shiraishi, 2004; sun bears, Scotson et al., 2017; giant pandas, Yong et al., 2004). Additionally, with the exception of sun bears, bears tend to be seasonal breeders, mating in spring (Northern hemisphere, approximately April-June) and summer (June-August), and giving birth in the winter (December-February) (Frederick et al., 2012; Spady et al., 2007). Giant pandas, however, have a shorter gestation and usually give birth in summer or fall (Schaller, 1985). Lastly, hibernation can be a factor in some bear species' seasonality. Sloth bears, Andean bears, southern Asiatic black bears, sun bears, and giant pandas do not hibernate (García-Rangel, 2012; Garshelis & Steinmetz 2020; Joshi et al., 1997; Nie et al., 2015; Scotson et al., 2017), but polar bears, northern Asiatic black bears, brown bears, and American black bears have a four- to six- month period of hibernation during the winter, which likely evolved as a way to survive during a period in which very little food was available (Garshelis & Steinmetz, 2020; Stirling & Derocher, 1990). A number of hormonal and metabolic changes are associated with hibernation, including lowered body temperature and heart rate (Nelson & Robbins, 2010), lowered metabolic rate (Watts & Jonkel, 1988) and altered serum composition (Barboza et al., 1997; Chow et al., 2013; Gardi et al., 2011; Spady et al., 2007). Therefore, one would expect that bear activity levels would vary with the change in seasons.

For bears living in human care, there is evidence from several case studies that both their behavior and physiology continue to exhibit seasonal variation. For example, a sloth bear housed at a zoo in India was observed to be more active in the winter (December-February) than the spring (March-May; Prajapati & Koli, 2020). Grizzly bears at Woodland Park Zoo in Seattle demonstrated higher pacing rates in the spring/summer (May-July) and higher activity levels in summer/fall (June-November; Fernandez et al., 2020). A black bear paced in different locations in the exhibit at different times of year, possibly in response to differing motivations between the seasons, such as mate-seeking behavior in spring/summer (May-July) and foraging in late summer/fall (August-November) (Carlstead & Seidensticker, 1991). Giant pandas selectively consumed different parts of bamboo depending on season (Hansen et al., 2009). Sloth bears living in a semi-captive bear rescue facility demonstrated seasonal changes in lipid values related to weight, potentially due to diet changes over the course of the year (Shanmugam et al., 2011). Zoo-housed Andean bears demonstrated seasonal changes in body weight, aligned with the natural breeding cycle rather than the ambient temperature (Gerstner et al., 2016). Grizzly bears and black bears in human care demonstrated hormonal and metabolic changes associated with hibernation (Barboza et al., 1997; Chow et al., 2013; Gardi et al., 2011; Nelson & Robbins, 2010; Spady et al., 2007; Watts & Jonkel, 1988). Thus, despite the homogeneity of zoo environments, bears still seem to demonstrate some responses to seasonal changes.

In addition to a potential disruption in bears' species-typical seasonal cycles, the zoo environment presents other factors that may affect behavior and welfare. Climate, diet, and habitat size have all been shown to affect bear behavior in zoos (Clubb & Mason, 2007; Spady et al., 2007; Watts, 2009). While the effect of these factors may vary by institution, an element of the zoo environment that is fundamentally different from the wild but persistent across zoos is the regular presence of large groups of unfamiliar humans (Sherwen & Hemsworth, 2019). The effect of zoo visitors on animal behavior and welfare has been studied in a wide range of taxa over the past thirty years with mixed results (Davey, 2007; Fernandez et al., 2009). Some studies have concluded that the presence of visitors was enriching for some species of primates (crowned lemurs, Jones et al., 2016; Diana monkeys, Todd et al., 2007). Others have noted that the presence of visitors or the associated increase in noise levels was linked with increases in undesirable behaviors, such as stereotypies, increased vigilance, or hiding (giraffes, elephants, and emus,

Jakob-Hoff et al., 2019; gorillas, Blaney & Wells, 2004; felids, Suárez et al., 2017; jaguars, Sellinger & Ha, 2005; koalas, Larsen et al., 2014).

Several studies have reported changes in zoo animal behavior due to the presence of visitors, without concluding that these changes indicated any particular effect on animal welfare (Bennett's wallabies, Beaudin-Judd et al., 2019; gorillas, Kuhar, 2008; Lewis et al., 2020; Stoinski et al., 2012; kangaroos, Sherwen et al., 2015), or found no effect of visitor presence (anteater, Chiapero et al., 2020; chimpanzees and gorillas, Bonnie et al., 2016; greater rheas, Azevedo et al., 2012; meerkats, Sherwen et al., 2014). In some cases, other factors in the environment have been found to be better predictors of animal behavior, such as temperature, weather, or time of day (African penguins, Ozella et al., 2017; hornbills, Rose et al., 2020; ring-tailed lemurs, Goodenough et al., 2019; tigers, Goldsborough, 2017), all of which typically co-vary with visitor density. Thus, historically, it has been challenging to tease apart visitor effects from the effects of concomitant changes in the environment or husbandry routines.

Bears have demonstrated mixed responses to visitor presence. Giant pandas and sun bears have been shown to be sensitive to the ambient noise created by crowds, especially during estrus and lactation, as measured by noise levels (giant pandas, Owen et al., 2004; sun bear, Owen et al., 2014). Giant pandas demonstrated less door-directed behavior when there were higher numbers of visitors at the habitat, as counted once per hour (Liu et al., 2017). Three polar bears demonstrated differential responses to visitor density, as measured by the number of visitors within 4m of the viewing window at the beginning of each observation: one bear demonstrated higher levels of stereotypy with higher visitor density, and the other two bears demonstrated lower levels of stereotypy (Kelly et al., 2015). Stereotypies are defined as “repetitive, unvarying and apparently functionless behavior patterns” (Mason, 1991, p. 103). Although an individual's performance of stereotypy is not necessarily indicative of an immediate welfare issue (Mason, 1991), increases in stereotypical behavior are often viewed as possible indicators of a negative welfare state, and managers use a variety of strategies to mitigate such behaviors (Bauer et al., 2013; Carlstead & Seidensticker, 1991; Mason et al., 2007; also see Watters, 2014). When visitors were present in front of their habitat, giant pandas at Zoo Atlanta demonstrated increases in exploration, feeding, object manipulation, stationary behavior, and time spent not visible to guests (Soriano et al., 2013). When visitors were present, brown bears at the Barcelona Zoo demonstrated increased locomotion, vigilance, stationary behavior, and stereotypy (Soriano et al., 2013). These studies reveal the importance of considering individual differences in responses to visitor density.

The purpose of the current study was to investigate the effects of season and two measures of visitor density on zoo-housed bear behavior and welfare. This study is broad in scope, covering ten individual bears of five different species, over a period of four years. A longitudinal bear behavior monitoring program was established at Cleveland Metroparks Zoo in June of 2017. In March of 2020, the spread of a novel coronavirus, COVID-19, was declared a pandemic by the World Health Organization (WHO, 2020). Due to this pandemic, Cleveland Metroparks Zoo was forced to close its doors to the public from March 17 – June 17, 2020. During this time, adjustments to staffing and new social distancing requirements allowed all non-visitor related zoo functions to continue. By separating two variables that are normally confounded in a zoo setting: the time of year (spring) and large groups of visitors, this unexpected zoo closure allowed us to opportunistically assess welfare in atypical conditions. Further, once the zoo reopened, visitor numbers remained limited, capped at half of the normal summer average attendance. We were also able to compare the effects of two measures of visitor density: crowd size at the habitat during observations, and zoo attendance on the day of the observation. Based on the natural history of these species, we predicted that bears would demonstrate higher activity levels in the warmer months (spring/summer, March-September), including foraging and locomotion, and possibly stereotypy. The mixed results of previous bear studies in only a few species made it difficult to predict whether we would expect to observe a difference in activity or stereotypy levels in relation to either measure of visitor density (Kelly et al., 2015; Soriano et al., 2013). Higher levels of activity, within species-typical ranges, are generally considered to be indicators of positive welfare, as are low levels of stereotypical behaviors.

## Method

### Subjects and Study Environment

This study was approved by the Animal Care and Use Committee of Cleveland Metroparks Zoo. Cleveland Metroparks Zoo (CMZ) in Cleveland, Ohio, USA, housed a total of ten bears between June 2017 and November 2020, including sloth bears ( $n = 3$ ), Andean bears ( $n = 2$ ), grizzly bears ( $n = 2$ ), American black bears ( $n = 2$ ), and a Malayan sun bear ( $n = 1$ ). Over the course of these four years, there were several changes to housing largely related to breeding season (see Table 1 for details).

**Table 1**

*Demographic Information and Group/Housing Changes for all Bears Housed at Cleveland Metroparks Zoo, 2017-2020*

Species	Subject name	Sex/age in 2017	Place of birth	Housing Conditions, 2017-2020
Andean bear ( <i>Tremarctos ornatus</i> )	Alfred	M, 22	Born at San Antonio Zoo (USA).	Alfred and Cayambe were housed as a breeding pair each year from approximately April-July. They were housed individually during the other months.
	Cayambe	F, 15	Born at Zoo de Cerza (France).	
Sloth bear ( <i>Melursus ursinus</i> )	Bala	M, 11	Born at Smithsonian National Zoo (USA).	Bala was solitary in June 2017 (due to death of the previous female). Shiva arrived in October 2017. They were housed as a breeding pair from March 2018 – October 2018. Shiva was given access to a birthing den over the winter, and gave birth to Shala in January 2019. Bala transferred to another zoo in September 2019. Shiva and Shala were housed together until October 2020.
	Shiva	F, 3	Born at Zoo Leipzig (Germany).	
	Shala	F, born Jan 2019	Born at CMZ.	
Sun bear ( <i>Helarctos malayanus</i> )	Scruffy	F, 32	Rescued from the pet trade in 1996.	Scruffy was housed at CMZ from 1996-2017, then transferred to another zoo. She returned to CMZ in November 2018.
Grizzly bear ( <i>Ursus arctos horribilis</i> )	Cody	M, 6	Rescued from the wild as cubs in 2011.	Housed as a pair continuously 2017-2020.
	Cooper	M, 6		
Black bear ( <i>Ursus americanus</i> )	Daisy	F, 21	Rescued from private ownership in 2006.	Housed as a pair continuously 2017-2020.
	V	F, 21		

The bears were housed in the Wilderness Trek section, which featured two sets of bear habitats. The “Tropical Bear” set of habitats housed Andean bears, sloth bears, and the sun bear. This area included three habitats of similar size (average 364.7 m<sup>2</sup>) that were visible to zoo visitors, and one small outdoor

habitat that was not visible to zoo visitors. Two of these habitats included small pools, and one included a ‘dig pit’: a converted pool filled with deep soil and mulch. All three habitats had large logs for climbing, hammocks, concrete and grass substrate, and were separated from zoo visitors with large moats (Figure 1). The “Temperate Bear” set of habitats was located on the other side of Wilderness Trek from the Tropical bears and housed the grizzly bears and black bears. This section included two habitats with large pools (average available space, including pools, 350 m<sup>2</sup>) and similar furniture (Figure 2). In June of 2018, wooden climbing structures were added to all three Tropical bear habitats, and to one of the Temperate bear habitats. These structures consisted of two large wooden platforms and were intended to increase elevated space in the habitats and provide additional shade.

**Figure 1**

*Tropical Bear Habitats, Left, Center, and Right*



*Note.* Wooden climbing structures, installed in June 2018, are visible in each photo to the right of the logs. Photos taken by LBK from the public viewing area.

**Figure 2**

*Temperate Bear Habitats, Left and Right*



*Note.* The left and center photos both depict the Left habitat. A wooden climbing structure, installed in June 2018, is visible in the far left photo. Photos taken by LBK from the public viewing area.

Prior to the beginning of this study, the animal care team introduced two husbandry strategies in an effort to maximize welfare by increasing novelty, space, and choice for all bear species. Following Rog et al. (2015), in which a sun bear demonstrated reduced visible pacing with access off-exhibit, all bears were given daily access to an off-exhibit holding area (a small, indoor concrete pen) starting in 2015. Access off-exhibit was available at all times, except during cleaning (approximately 1 hr per day). Further, rather than being restricted to the indoor holding building at night, bears were given access to their outdoor habitats at night, within set temperature limits: Andean, sloth, and sun bears were given access to the outdoors during the day and overnight unless the temperature dropped below 40 °F. Grizzly

bears and black bears were given access outdoors during the day and overnight regardless of the outdoor temperature as long as the temperature in the holding building stayed above 40 °F. At the discretion of the keepers, all bears could also be restricted to the indoor holding building in the case of inclement weather. In 2016, with the goal of increasing variability, animal management began to rotate bears between different habitats on a daily basis. Andean bears, sloth bears, and the sun bear were rotated between the three Tropical bear habitats (with some exceptions for medical reasons and when the sloth bear cub was an infant), and the grizzly bears and black bears were rotated between the two Temperate bear habitats. For all bears, rotation occurred regularly during the warmer months (approximately March-November) and ceased during the winter.

The diets offered to the bears varied by species and season. All bears received a portion of Mazuri Wild Carnivore diet on a daily basis, with the amount varying by species and appetite – keepers observed the amount of food consumed each day, weighed the bears every two weeks, and adjusted the diet up or down as needed on a weekly basis. The types of greens, vegetables, and produce offered varied seasonally based on availability. Sloth, Andean, grizzly, and black bears were all offered bones once per week and the sun bear was offered ribs once per week. Grizzly and black bears were also given rabbits weekly, and 0.25 lb. horse meat daily, used during training sessions. Grizzly and black bears displayed some seasonal food preferences; in the winter, compared to other seasons, they consumed far less grain and produce, grizzly bears refused melon, and black bears refused most produce, besides apples. These diets were in line with current AZA recommendations (AZA Bear TAG, 2019).

## Data Collection

Data collection commenced in June, 2017, and concluded in November, 2020. Bears were observed live using the iPad application ZooMonitor (Ross et al., 2016) on iPad minis (Apple, Inc.). Observations occurred Monday through Friday, during hours that the Zoo was open to the public (10:00-17:00) at least twice a week and no more than once per time period (morning, 10:00-13:00; afternoon, 13:00-17:00), per day. Bears were observed only from the public areas and when they had access to their outdoor habitats. Access on and off the habitat and the location of each individual were ascertained at the beginning of each observation by contacting the keeper on duty. All bears were observed on every observation day (barring medical exams or other exceptions). Observers followed a randomized schedule so that bears were not observed in the same order every day, and observations were approximately balanced between morning and afternoon. At the beginning of each observation, the observer recorded date, time, weather, temperature, habitat, access status, housing, pool status, and crowd size. Crowd size was determined by counting the number of zoo visitors within one meter of the habitat at the beginning of the observation and was originally categorized as follows: no visitors, 1-10 visitors, 11-20 visitors, 21-30 visitors, 31 or more visitors. As the 0 and 1-10 visitor categories were the most common, crowd sizes were collapsed for analysis as follows: none (zero visitors; 213 hrs), low (1-10 visitors; 215 hrs), and high (11 or more visitors; 34 hrs; Table 2).

Behavior data were collected using 10-min focal follows in which behaviors were noted at 30-s intervals. Observers utilized an exhaustive ethogram for data collection, which was condensed into six behavior categories for analysis (Table 3). As an additional measure of visitor density, daily attendance numbers were obtained from the Zoo's Guest Services records and divided into three categories: low (1-1000 visitors,  $M = 534 \pm 258$ , 180 hours), medium (1001-4000 visitors,  $M = 2304 \pm 918$ , 203 hrs), and high (4001+ visitors,  $M = 6265 \pm 2219$ , 79 hrs).

All observers were trained by LBK to recognize each bear individually and to collect data for the project. Before their data could be added to the dataset, all observers had to pass a reliability test. This test consisted of using the ethogram to score a total of six bear videos that had previously been scored and entered into the dataset by LBK. 85% or more of data points had to be in agreement before the observer was considered reliable. Following this test, observers were not further tested for reliability. Over the course of the study, 22 additional observers contributed to the dataset.

**Table 2***Independent Variables Collected by Observers at the Beginning of each Focal Observation*

Variable	Description	Reporting options
Date	Date of the observation	DD/MM/YYYY
Time	Time of the observation	10:00-17:00
Weather	Weather at the beginning of the observation	Sun, Clouds, Overcast, Rain, Snow
Temperature	Temperature at the beginning of the observation	Ascertained using observer's phone; reported in degrees Fahrenheit
Access	Status at the beginning of the observation – bears were generally given access off-exhibit at all times of day, however, this could vary with keeper cleaning schedules	Two options: in/out or habitat only. This was ascertained ahead of time by calling zookeepers prior to beginning the observation
Habitat	Location of bear at the beginning of the observation	Four possible habitat options for Tropical bears: Left, Center, Right, Multiple (access to Center and Right). Two possible habitat options for Temperate bears: Left, Right
Housing	Status at the beginning of the observation – whether the bear was housed with a social partner or not	Two options: solitary or pair
Pool status	Status at the beginning of the observation – whether the pool in the habitat was filled with water	Four options: Empty, partially filled (50% or less), full, unknown
Crowd size	The number of zoo visitors within one meter of the habitat at the beginning of the observation	Options: None: zero zoo visitors Small: 1-10 zoo visitors Large: 11 + zoo visitors
Season	Standardized across years; added to dataset post-data collection	Spring: March 21-June 20 Summer: June 21-September 20 Autumn: September 21-December 20 Winter: December 21-March 20
Daily zoo attendance	Added to dataset post-data collection	Low: 1-1000 zoo visitors Medium: 1001-4000 zoo visitors High: 4001+ zoo visitors



**Table 3***Behavioral Ethogram Used to Collect Bear Behavior Data*

Behavior	Definition
Visible	Individual is visible in the habitat from the public viewing area.
Stereotypy	Individual is performing stereotypic, repeated behavior, including pacing (defined as locomotion across the same path, repeated at least three times (ABA)), head rolling, or swaying/rocking.
Social	Individual interacts with conspecific. Can be affiliative or agonistic.
Foraging	Individual sniffs or manipulates environment, object, or building, or consumes food. Includes all feeding behavior, as well as all object manipulation for the purpose of obtaining or processing food. This behavior took precedence over locomotion.
Locomotion	Individual moves at least one body length at any speed, on land or in water, while not performing any other activity (such as social play or foraging).
Inactive	Individual is still and performing no other behaviors. Can be standing, sitting, alert, passive, or lying down.

**Data analysis***Crowd Size and Daily Attendance by Year*

All analyses were completed in R Version 4.0.3 (R Core Team, 2020). To investigate whether crowd size at the habitats and daily attendance at the zoo varied with season and year, we conducted two generalized linear models (GLM) using package lme4 (Bates et al., 2015). Both models included season, year, and the interaction of season and year as fixed factors. Package emmeans (Lenth, 2020) was used to ascertain the estimated marginal means and the contrasts of the model, with a Tukey adjustment for multiple comparisons.

*Visibility and Behavior*

Visibility was calculated as the total number of intervals per observation in which the bear was visible in the habitat divided by twenty (the total number of intervals). Stereotypy, foraging, locomotion, and inactivity were calculated as a percentage of visible intervals in which the bear performed the behavior divided by the total number of visible intervals. Social behavior was calculated as a percentage of visible intervals in which the bear performed the behavior divided by the total number of visible intervals when housed with another bear. For the models including social behavior, the sun bear was not included, as she was not housed with another bear at any time during the study.

We used generalized linear mixed models (GLMM) to examine the effects of season, visitor density, and year on bear behavior. Individual models were run separately for each behavior in the ethogram (visibility, stereotypy, social behavior, foraging, locomotion, and inactivity). As time of day, temperature, weather, and access off-exhibit could also have had an effect on behavior, these were taken into account in the models. All models were run twice in order to investigate visitor density in two ways: the first set included crowd size, season, year, interaction of season and year, time, temperature, weather, and access off-exhibit as fixed factors, and the second set of models differed only in that they included daily attendance instead of crowd size (due to model convergence issues, crowd size and daily attendance could not be included in the same models). For both sets of models, subject and habitat were included as random factors. Factors were removed and models compared using AIC scores to determine the best fitting model for each behavioral outcome (model details in Table 4).



**Table 4***Fixed Factors Included in All GLMMs for Bear Behavior*

Behavior	Fixed factors included in the crowd size and daily attendance models
Visibility	Crowd size or daily attendance, season, year, season*year, time, temperature
Stereotypy	Crowd size or daily attendance, season, year, season*year, temperature
Social	Crowd size or daily attendance, season, year, season*year, temperature
Foraging	Crowd size or daily attendance, season, year, season*year, time, temperature, weather, access
Locomotion	Crowd size or daily attendance, season, year, season*year, time, temperature, weather, access
Inactive	Crowd size or daily attendance, season, year, season*year, time, temperature, access

All GLMMs were run using the beta distribution, which is appropriate for proportion data such as this (Ferrari & Cribari-Neto, 2004). In order to use the beta distribution in R, all zeros in the dataset were converted to 0.0000001, and all ones in the dataset were converted to 0.9999999. Residual QQ plots were checked for normality (Pereira, 2019). We used the package *glmmTMB* (Brooks et al., 2017) to run the GLMMs, and *emmeans* (Lenth, 2020) for estimated marginal means and pairwise contrasts, using the Tukey adjustment for multiple comparisons. Multicollinearity of variables was tested using the ‘*check\_collinearity*’ function of package *performance* (Lüdtke et al., 2020).

## Results

An average of 45.7 hrs of data was collected per bear, from June 2017–November 2020 (Table 5).

**Table 5***Number of Hours of Data Collected per Individual, Across All Seasons*

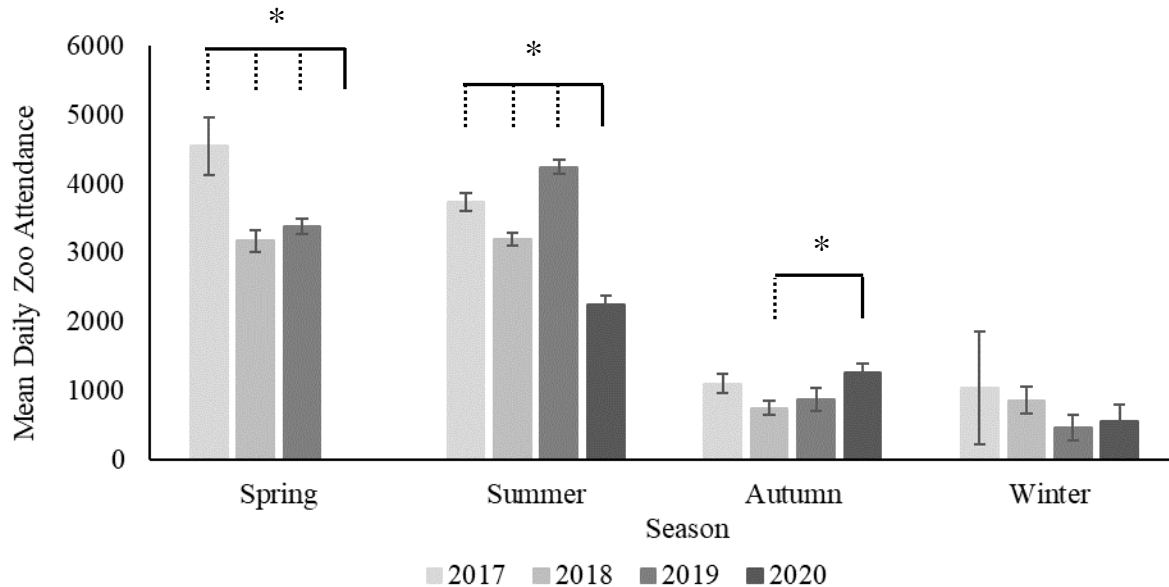
Species	Subject	Number of follows	Total hours	Spring hours	Summer hours	Autumn hours	Winter hours
Andean	Alfred	321	53.5	12.7	24.5	14.3	2.0
	Cayambe	372	62.0	13.3	28.5	16.7	3.5
Sloth	Bala	234	39.0	6.3	19.3	10.3	3.0
	Shiva	283	47.2	11.2	20.5	13.0	2.5
	Shala	137	22.8	4.0	11.2	7.2	0.5
Sun	Scruffy	66	11.0	3.2	4.3	3.2	0.3
Grizzly	Cody	384	64.0	11.0	22.5	18.7	11.8
	Cooper	385	64.2	10.8	23.2	18.5	11.7
Black	Daisy	279	46.5	8.2	19.5	15.8	3.0
	V	279	46.5	7.7	20.5	15.3	3.0

### Crowd size and daily attendance across years

Crowd sizes at the habitats were lower in 2020 than in other years ( $F(9, 2750) = 263.329, p < .001$ ). Daily attendance was lower in spring and summer 2020 than spring and summer of the other three years ( $F(9) = 31.502, p < .001$ ; Figure 3).

**Figure 3**

*Mean Daily Zoo Attendance across Seasons and Years*



*Note.* Data drawn from Cleveland Metroparks Zoo's Guest Services records of daily zoo attendance from June 2017-November 2020. Seasons were defined as: spring (March 21-June 20), summer (June 21-September 20), autumn (September 21-December 20), and winter (December 21-March 20). Solid and dotted lines indicate direction of effect (i.e., attendance in spring 2020 was significantly lower than attendance in the springs of 2017, 2018, and 2019, but attendance in the springs of those three years were not different from each other). Standard error bars represent standard error of the mean. Asterisk notes significant differences at  $\alpha = .05$ .

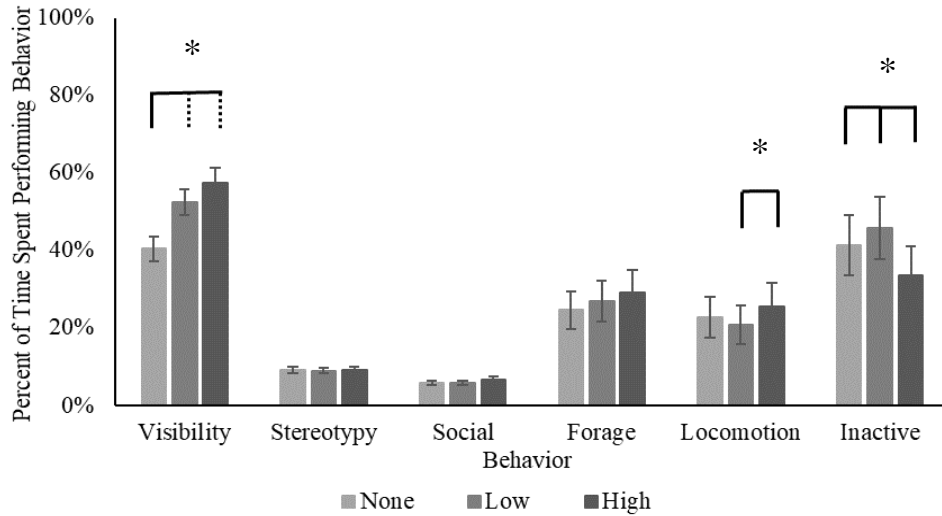
### Visibility

Bear visibility to guests was predicted by crowd size, season, year, and the interaction of season and year (crowd size:  $F(2, 2744) = 38.457, p < .001$ ; season:  $F(3, 2744) = 3.541, p = .014$ ; year:  $F(3, 2744) = 4.636, p = .003$ ; season by year:  $F(9, 2744) = 2.001, p = .035$ ). Bears were more visible to guests when crowds of any size were present than when no visitors were present (none vs small:  $T(2744) = 8.075, p < .001$ ; none vs large:  $T(2744) = 6.151, p < .001$ ; Figure 4).

There was a main effect of season: bears were more visible to guests in the spring compared to winter ( $T(2744) = 2.970, p = .020$ ; Figure 5). There was also a main effect of year: bears were more visible in 2020 than 2018 ( $T(2744) = -3.438, p = .003$ ). However, these main effects were qualified by a significant interaction of season and year. There was an effect of year only in the summer season: bears were more visible to guests in the summer of 2020 than in the summer of 2018 ( $T(2744) = -3.907, p < .001$ ). This was the case in the daily attendance model as well (main effect:  $F(9, 2745) = 2.657, p = .005$ ; summer of 2018 vs summer of 2020:  $T(2745) = -3.799, p < .001$ ). There was no effect of either time or temperature on bear visibility (time:  $F(1, 2744) = .202, p = .653$ ; temperature:  $F(1, 2744) = 1.742, p = .187$ ).

**Figure 4**

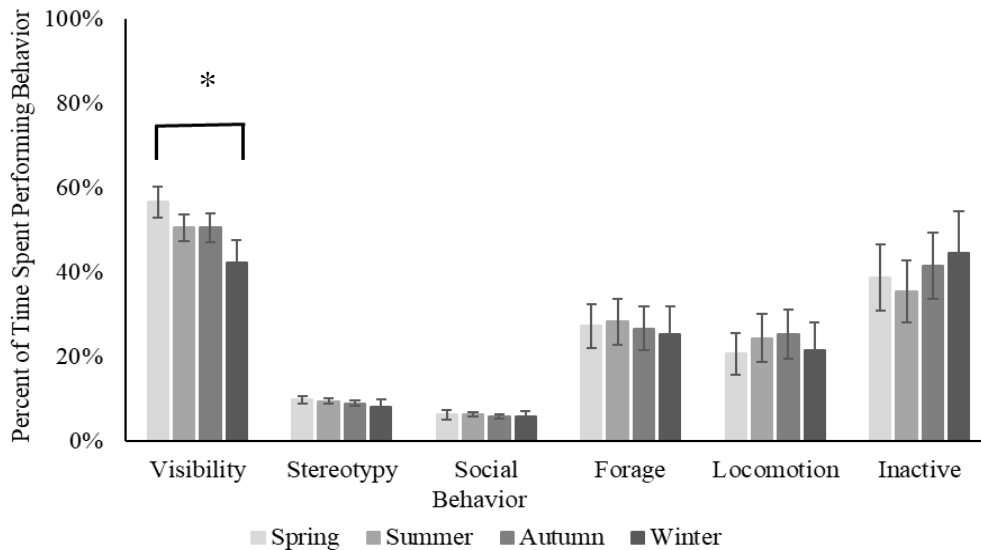
*Mean Percentage of Time Spent in Behaviors across Crowd Sizes*



*Note.* Data drawn from estimated marginal means for the percent of time bears at Cleveland Metroparks Zoo spent visible in the habitat, and performing observed behaviors. Data were collected from June 2017 – November 2020. Crowd sizes were defined as none (zero visitors), low (1-10 visitors), and high (11 or more visitors). Stereotypy, foraging, locomotion, and inactivity percentages were all calculated as a percentage of visible time. Social behavior was calculated as a percentage of visible time when bears were housed together. Solid and dotted lines indicate direction of effect (i.e., bear visibility with no crowds was significantly lower than visibility with either low or high crowds, but visibility levels during low and high crowds were not different from each other). Standard error bars represent standard error of the mean. Asterisk notes significant differences at alpha = .05.

**Figure 5**

*Mean Percentage of Time Spent in Behaviors across Seasons*



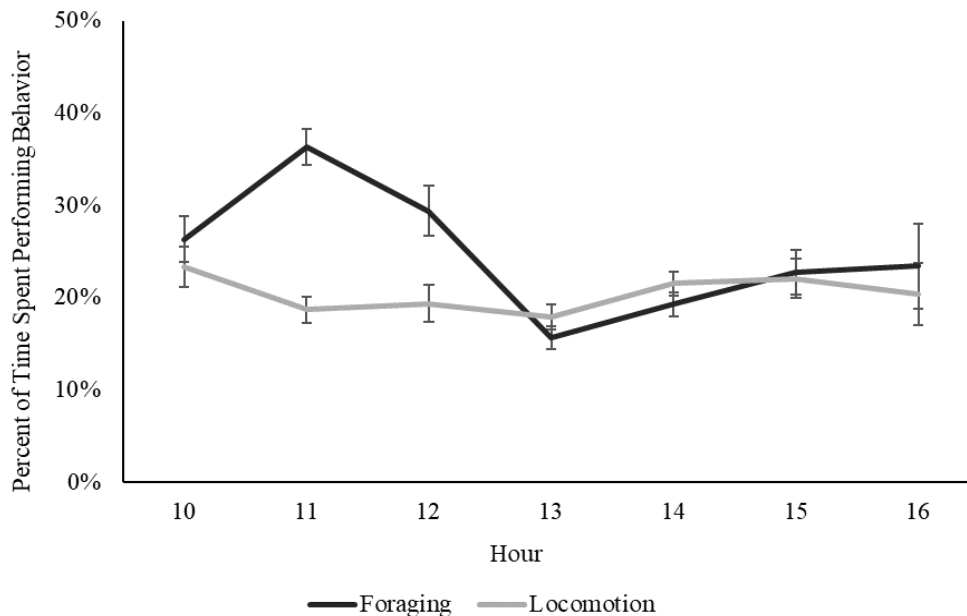
*Note.* Data drawn from estimated marginal means for the percent of time bears at Cleveland Metroparks Zoo spent visible in the habitat, and performing observed behaviors. Data were collected from June 2017 – November 2020. Seasons were defined as spring (March 21-June 20), summer (June 21-September 20), autumn (September 21-December 20), and winter (December 21-March 20). Stereotypy, foraging, locomotion, and inactivity percentages were all calculated as a percentage of visible time. Social behavior was calculated as a percentage of visible time when bears were housed together. Standard error bars represent standard error of the mean. Asterisk notes significant differences at alpha = .05.

## Foraging

The percent of time bears spent foraging was predicted by time of day ( $F(1, 1843) = 9.845, p = .002$ ). Bears foraged more earlier in the day ( $Est. -.0006, Z = -3.138, p = .002$ ; Figure 6). There were no differences in foraging levels across crowd sizes, seasons, years, temperature, weather, availability of access, or in association with daily attendance categories (crowd size:  $F(2, 1843) = 2.496, p = .083$ ; season:  $F(3, 1843) = .322, p = .810$ ; year:  $F(3, 1843) = .294, p = .829$ ; temperature:  $F(1, 1843) = .214, p = .644$ ; weather:  $F(6, 1843) = 1.296, p = .256$ ; access:  $F(6, 1843) = .658, p = .577$ ; daily attendance:  $F(2, 1843) = .319, p = .727$ ).

**Figure 6**

*Mean Percentage of Time Spent in Foraging and Locomoting by Time*



*Note.* Bear behavior data were collected at Cleveland Metroparks Zoo from June 2017 – November 2020. Data were collected during public hours, from 10:00-17:00, Monday-Friday. Foraging and locomotion percentages were calculated as a percentage of visible time. Standard error bars represent standard error of the mean.

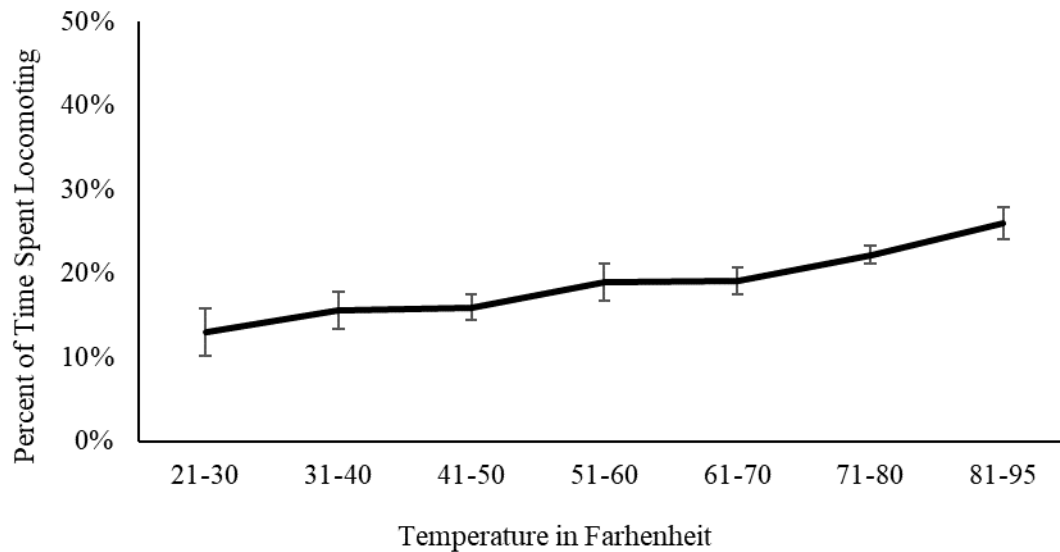
## Locomotion

The percent of time bears spent locomoting was predicted by crowd size, time, and temperature (crowd size:  $F(2, 1843) = 3.703, p = .025$ ; time:  $F(1, 1843) = 4.433, p = .035$ ; temperature:  $F(2, 1843) = 6.544, p = .011$ ). Bears spent more time locomoting when large crowds were present compared to when small crowds were present ( $T(1843) = 2.437, p = .040$ ; Figure 4). Bears locomoted more in the earlier part of the day ( $Est. = .0004, Z = 2.105, p = .035$ ; Figure 6) and at higher temperatures ( $Est. = -.0073, Z = 2.558, p = .011$ ; Figure 7).

Bears demonstrated no differences in levels of locomotion across seasons, years, weather, availability of access, or in association with daily attendance categories (season:  $F(3, 1843) = 1.920, p = .124$ ; year:  $F(3, 1843) = .631, p = .595$ ; weather:  $F(6, 1843) = 1.438, p = .196$ ; access:  $F(3, 1843) = 1.066, p = .362$ ; daily attendance:  $F(2, 1843) = 1.767, p = .171$ ).

**Figure 7**

Mean Percentage of Time Spent Locomoting by Temperature



*Note.* Bear behavior data were collected at Cleveland Metroparks Zoo from June, 2017 – November, 2020. Data were collected during public hours, from 10:00-17:00, Monday-Friday. Locomotion percentages were calculated as a percentage of visible time. Standard error bars represent standard error of the mean.

### Inactivity

The percent of time bears spent inactive was predicted by crowd size and year (crowd size:  $F(2, 1849) = 11.458, p < .001$ ; year:  $F(3, 1849) = 3.747, p = .010$ ). Bears spent less time inactive when large crowds were present at the habitat compared to when small crowds or no crowds were present, and when no crowds were present compared to small crowds (large vs small:  $T(1849) = -4.435, p < .001$ ; large vs none:  $T(1849) = -2.603, p = .025$ ; none vs small:  $T(1849) = 2.538, p < .030$ ; Figure 4), and less time inactive in 2017 compared to 2019 ( $T(1849) = -3.094, p = .011$ ). However, there were no differences in inactivity levels between 2020 and any of the previous three years (2017 vs 2020:  $T(1849) = -2.378, p = .082$ ; 2018 vs 2020:  $T(1849) = -.096, p = 1.000$ ; 2019 vs 2020:  $T(1849) = 1.655, p = .348$ ) and no interaction between year and season.

The percent of time bears spent inactive was also predicted by daily attendance ( $F(2, 1843) = 3.453, p = .032$ ). Inactivity was lower on days of high daily attendance compared to medium attendance ( $T(2, 1843) = -2.616, p = .024$ ).

There were no differences in inactivity across seasons, time, temperature, or availability of access (season:  $F(3, 1849) = 2.276, p = .078$ ; time:  $F(1, 1849) = 1.190, p = .276$ ; temperature:  $F(1, 1849) = 1.461, p = .227$ ; access:  $F(3, 1849) = 1.108, p = .345$ ).

### Stereotypy and Social Behavior

There were no differences in the percentage of time bears spent performing stereotypical behaviors or social behaviors across crowd sizes, seasons, years, temperature, or in association with daily attendance categories (stereotypy: crowd size:  $F(2, 1853) = .069, p = .933$ ; season:  $F(3, 1853) = .452, p = .716$ ; year:  $F(3, 1853) = .416, p = .741$ ; temperature  $F(1, 1853) = .271, p = .995$ ; daily attendance:  $F(2, 1854) = .117, p = .890$ . Social behavior: crowd size:  $F(2, 1465) = 1.337, p = .263$ ; season:  $F(3, 1465) = .288, p = .834$ ; year:  $F(3, 1465) = .073, p = .975$ ; temperature:  $F(1, 1465) = .135, p = .714$ ; daily attendance:  $F(2, 1465) = .143, p = .867$ ).

## Discussion

We systematically observed ten individuals of five bear species in a zoo environment for almost four years and found limited effects of season, crowd size at the habitat, and daily zoo attendance on bear behavior. Despite the disruption of COVID-19 and the associated zoo closure, we observed no behavioral differences between a spring and summer of limited visitors and the three previous years, except that bears were more visible to guests in the summer of 2020 than in the summer of 2018. We did observe limited differences in activity levels associated with large crowd sizes and limited seasonal differences in behavior, but the lack of any other interactions of season and year suggest that previously reported seasonal changes in zoo bear behavior may not have been attributable to varying crowd sizes between seasons.

The effects of season and visitor density on animal behavior are often confounded, but due to the zoo closure caused by COVID-19, we had the opportunity to tease these factors apart. We observed overall effects of crowd size and season: bears were more visible to guests, i.e., they chose to spend more time in their habitats when visitors were present, whether the crowds at the habitat were small or large, and more visible in the spring than in winter. Further, we found that bears were more visible to guests during the summer of 2020 than the summer of 2018. However, although no visitors were present in the spring of 2020 and visitor numbers in the autumn and winter were similar to those of other years, we found no other interactions of season and year. Other studies conducted during zoo closures in 2020 have found individual differences in animals' responses to the sudden lack of visitors, with some individuals demonstrating increased space use and environmental interactions, and others demonstrating no differences (Williams et al., 2021a, b). This suggests that the lack of zoo visitors during the COVID-19 pandemic did not have a substantial effect on bear behavior.

We observed limited differences in foraging and locomotion by time and temperature. Bears foraged and locomoted more during the earlier part of the day, and locomoted more when temperatures were higher. This may be related to daily routines, as keepers typically scattered a large portion of the bears' daily diet in the outdoor habitat in the morning before bears were granted access. Seasonally, although the amount of food presented to the bears at CMZ was reduced in the colder months, we observed that foraging rates remained similar across the year. This may in part be driven by underlying species differences. Grizzly and black bears showed less interest in food in the winter than in the summer (Jen DeGroot, pers. comm.), but Andean, sloth, and sun bears' appetites appeared to be more consistent across the year. On warmer winter days, tropical bears were given access to their outdoor habitats, and on those days, their foraging rates were likely similar to other times of year. Other studies of bears in zoos have found variation in rates of foraging and stereotypy by season and visitor presence (Fernandez et al., 2020; Liu et al., 2017; Soriano et al., 2013), but we found that rates of foraging, stereotypy and social behaviors did not vary by season, crowd size, or daily attendance.

Bears were observed locomoting more when large crowds were present and were less inactive with high daily attendance (4000+ visitors) and large crowd sizes (11+ visitors) at the habitat. Lower levels of inactivity combined with higher levels of visibility and locomotion suggests that bears were more active in the presence of large crowds. A previous study reported that brown bears demonstrated increased activity and stereotypy in association with visitor presence (Soriano et al., 2013). However, it is difficult to tease apart the direction of this effect. It is possible that bears responded to the increased noise caused by groups of people by entering their outdoor habitats. Noise has been associated with increased agitation and vigilance in some species (apes, Hashmi & Sullivan, 2020; koalas, Larsen et al., 2014; giant pandas, Owen et al., 2004; primates, ocelot, red deer, Quadros et al., 2014). Although we were unable to quantify noise levels in this study, others have demonstrated that large crowds are associated with higher noise levels in zoos (Hashmi & Sullivan, 2020). However, studies of visitor preferences have shown that guests are attracted to active animals (Altman, 1998), and due to the general association between season and visitor numbers (i.e., more guests were present at the habitats and at the zoo on a daily basis during

the seasons in which bears were more active), and the fact that higher visibility was also associated with crowds, it may be more likely that the crowds gathered in response to the bears' presence in the habitat.

Both the higher visibility in the spring and the higher levels of locomotion with warmer temperatures may be related to natural history. All five species follow various seasonal ranging patterns in the wild, and the warmer months coincide with the time that all species would be active, foraging for new growth and ripening fruit (Costello et al., 2016; García-Rangel, 2012; Joshi et al., 1997; Scotson et al., 2017) and seeking mates (Spady et al., 2007). Bears' energy levels tend to rise with the increase in temperature and lengthening photoperiod (García-Rangel, 2012; Joshi et al., 1997; Nelson et al., 1983). The fact that we found no interactions of season and year for any behavior other than visibility suggests that these seasonal responses were not being driven by visitors and were instead likely driven by these ambient environmental factors.

Overall, we observed few differences in bear behavior between seasons and varying visitor densities. This may be due, in part, to the interactions of several management and husbandry strategies. As multiple bear studies have demonstrated that having the choice to access off-exhibit areas can reduce rates of stereotypical behavior (Rog et al., 2015; Ross, 2006), bears at CMZ are given regular access off-exhibit. These bears are also regularly rotated between different habitats, a strategy that has been associated with increased activity levels, space use, and decreased stereotypy in some species (Lukas et al., 2003; Ryan, 2016; White et al., 2003). The bears also receive daily, varied enrichment, which has been shown to have positive effects on behavior, including increased activity and reduced stereotypy (Law & Reid, 2010; Wagman et al., 2018). The combination of these strategies may be related to the relatively low rates of stereotypy compared to foraging and locomotor activity that we observed. During the zoo closure, all of these strategies continued unchanged. This consistency in routine may have contributed to the lack of behavioral differences between 2020 and other years, despite the difference in visitor density.

There were some limitations in this study. Despite the breadth of our study including several species studied over a significant period of time, we observed only one or two individuals of each species, limiting our ability to draw species level comparisons. This limitation may result in an overgeneralization of the similarities between species and an underestimation of the variation between species that have different natural histories, diets, and behaviors in the wild. Further, low rates, and therefore reduced variability, of some behaviors, such as stereotypy and social behavior, and the lower number of observations collected during high crowd sizes and spring of 2020 may have reduced our ability to detect effects of predictors in our models. Furthermore, since not all bears were housed socially, we were limited in our ability to draw conclusions concerning the frequency of social behaviors. Finally, given the correlational nature of our data, we cannot draw causal inferences regarding the effects of our predictors. For example, bears may be visible more often when crowd sizes are larger because crowds are drawn to more active bears rather than bears being more active in the presence of larger crowds.

We evaluated two measures of visitor density as possible predictors of bear behavior: crowd size at the habitat during each observation, and the average attendance for the day of the observation. Some studies have suggested that counting visitors close to the habitat (as we did with our measure of crowd size) may provide a more sensitive prediction of behavior change than a broad measure of daily attendance (Kuhar, 2008; Lewis et al., 2020). Although we found limited differences between the two measures, this could be due to the limited differences we observed overall. Future studies of visitor effects that include multiple methods of quantifying visitors could continue to elucidate the differences between these types of measures.

We observed limited differences in bear visibility and behaviors by season, time of day, and temperature, in line with what would be expected based on natural history. We also observed limited differences in behavior associated with large crowd sizes and high daily attendance, consistent with patterns of visitor interest in viewing active animals, and we observed higher bear visibility during the summer of 2020 compared to the summer of 2018, but no behavioral differences between the spring that the Zoo was closed and the three previous spring seasons in the dataset. These results suggest that season and visitor density did not influence bear welfare at Cleveland Metroparks Zoo, at least as indicated by



behavior and habitat use measures. This study benefited from the comparatively large number of bears housed at Cleveland Metroparks Zoo relative to other zoos, but future studies that include more individuals across multiple institutions could illuminate important differences between species, management styles, or regions of the country. Welfare indicators besides behavior such as markers of physiology or health including reproductive and metabolic hormones, or weight and body condition, would add valuable information to our understanding of how seasonality continues to affect bears in zoos. All of these factors will be important to take into consideration as we continue to study and improve the lives of bears in human care.

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### References

- Ali, A., Zhou, Z., Waseem, M., Khan, M. F., Ali, I., Asad, M., & Qashqaei, A. T. (2017). An assessment of food habits and altitudinal distribution of the Asiatic black bear (*Ursus thibetanus*) in the Western Himalayas, Pakistan. *Journal of Natural History*, *51*(11–12), 689–701. <https://doi.org/10.1080/00222933.2017.1303097>
- Altman, J. D. (1998). Animal activity and visitor learning at the zoo. *Anthrozoös*, *11*(1), 12–21. <https://doi.org/10.1080/08927936.1998.11425083>
- AZA Bear TAG (2019). *Sun and sloth bear care manual*. <https://www.aza.org/animal-care-manuals>
- Azevedo, C. S. de, Lima, M. F. F., Silva, V. C. A. da, Young, R. J., & Rodrigues, M. (2012). Visitor influence on the behavior of captive greater rheas (*Rhea americana*, *Rheidae aves*). *Journal of Applied Animal Welfare Science*, *15*(2), 113–125. <https://doi.org/10.1080/10888705.2012.624895>
- Barboza, P. S., Farley, S. D., & Robbins, C. T. (1997). Whole-body urea cycling and protein turnover during hyperphagia and dormancy in growing bears (*Ursus americanus* and *U. arctos*). *Canadian Journal of Zoology*, *75*(12), 2129–2136. <https://doi.org/10.1139/z97-848>
- Bauer, E., Babitz, M., Boedeker, N., & Hellmuth, H. (2013). Approaches to understanding and managing pacing in sloth bears in a zoological setting. *International Journal of Comparative Psychology*, *26*(1), 53–74. <https://doi.org/10.5070/P4261020186>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. <http://doi.org/10.18637/jss.v067.i01>
- Beaudin-Judd, J., Weladji, R. B., Lazure, L., & Paré, P. (2019). Activity budget and spatial distribution of Bennett's wallabies (*Macropus rufogriseus*) in open versus closed exhibit designs. *Zoo Biology*, *38*(3), 258–265. <https://doi.org/10.1002/zoo.21486>
- Blaney, E., & Wells, D. (2004). The influence of a camouflage net barrier on the behaviour, welfare and public perceptions of zoo-housed gorillas. *Animal Welfare*, *8*, 111–118.
- Bonin, M., Dussault, C., & Côté, S. D. (2020). Increased trophic position of black bear (*Ursus americanus*) at the northern fringe of its distribution range. *Canadian Journal of Zoology*, *98*(2), 127–133. <https://doi.org/10.1139/cjz-2019-0062>
- Bonnie, K. E., Ang, M. Y. L., & Ross, S. R. (2016). Effects of crowd size on exhibit use by and behavior of chimpanzees (*Pan troglodytes*) and Western lowland gorillas (*Gorilla gorilla gorilla*) at a zoo. *Applied Animal Behaviour Science*, *178*, 102–110. <https://doi.org/10.1016/j.applanim.2016.03.003>
- Brooks M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler M., & Bolker B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated

- generalized linear mixed modeling. *The R Journal*, 9(2), 378-400. <https://doi.org/10.3929/ethz-b-000240890>
- Cabana, F., Yusof, O., Kawi, J., Li, D., Huang, Y., Wang, P., & Tay, T. (2020). Seasonal diet switching in captive giant pandas. *Ursus*, 2020(31e4), 1-8. <https://doi.org/10.2192/URSUS-D-17-00023.5>
- Carlstead, K., & Seidensticker, J. (1991). Seasonal variation in stereotypic pacing in an American black bear *Ursus americanus*. *Behavioural Processes*, 25(2-3), 155-161. [https://doi.org/10.1016/0376-6357\(91\)90017-T](https://doi.org/10.1016/0376-6357(91)90017-T)
- Chiapero, F., Ferrari, H. R., Prieto, M. V., García Capocasa, M. C., & Busso, J. M. (2020). Multivariate analyses of the activity pattern and behavior of the lesser anteater on open and closed days at Córdoba Zoo, Argentina. *Journal of Applied Animal Welfare Science*, 24(1), 83-97. <https://doi.org/10.1080/10888705.2020.1799214>
- Chow, B. A., Donahue, S. W., Vaughan, M. R., McConkey, B., & Vijayan, M. M. (2013). Serum immune-related proteins are differentially expressed during hibernation in the American black bear. *PLOS ONE*, 8(6), 9. <https://doi.org/10.1371/journal.pone.0066119>
- Clubb, R., & Mason, G. J. (2007). Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. *Applied Animal Behaviour Science*, 102(3-4), 303-328. <https://doi.org/10.1016/j.applanim.2006.05.033>
- Costello, C. M., Cain, S. L., Pils, S., Frattaroli, L., Haroldson, M. A., & van Manen, F. T. (2016). Diet and macronutrient optimization in wild ursids: A comparison of grizzly bears with sympatric and allopatric black bears. *PLOS ONE*, 11(5), e0153702. <https://doi.org/10.1371/journal.pone.0153702>
- 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>
- Ferguson, S. H., Taylor, M. K., Born, E. W., Rosing-Asvid, A., & Messier, F. (1999). Determinants of home range size for polar bears (*Ursus maritimus*). *Ecology Letters*, 2(5), 311-318. <https://doi.org/10.1046/j.1461-0248.1999.00090.x>
- Fernandez, E. J., Yoakum, E., & Andrews, N. (2020). Seasonal and daily activity of two zoo-housed grizzly bears (*Ursus arctos horribilis*). *Journal of Zoological and Botanical Gardens*, 1(1), 1-12. <https://doi.org/10.3390/jzbg1010001>
- 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>
- Ferrari, S., & Cribari-Neto, F. (2004). Beta regression for modelling rates and proportions. *Journal of Applied Statistics*, 31(7), 799-815. <https://doi.org/10.1080/0266476042000214501>
- Frederick, C., Hunt, K. E., Kyes, R., Collins, D., & Wasser, S. K. (2012). Reproductive timing and aseasonality in the sun bear (*Helarctos malayanus*). *Journal of Mammalogy*, 93(2), 522-531. <https://doi.org/10.1644/11-MAMM-A-108.1>
- Fredriksson, G. M., Wich, S. A., & Trisno. (2006). Frugivory in sun bears (*Helarctos malayanus*) is linked to El Niño-related fluctuations in fruiting phenology, East Kalimantan, Indonesia: Phenological influences on sun bear frugivory. *Biological Journal of the Linnean Society*, 89(3), 489-508. <https://doi.org/10.1111/j.1095-8312.2006.00688.x>
- Galicia, M. P., Thiemann, G. W., Dyck, M. G., & Ferguson, S. H. (2015). Characterization of polar bear (*Ursus maritimus*) diets in the Canadian High Arctic. *Polar Biology*, 38(12), 1983-1992. <https://doi.org/10.1007/s00300-015-1757-1>
- García-Rangel, S. (2012). Andean bear *Tremarctos ornatus* natural history and conservation: Andean bear natural history and conservation. *Mammal Review*, 42(2), 85-119. <https://doi.org/10.1111/j.1365-2907.2011.00207.x>
- Gardi, J., Nelson, O. L., Robbins, C. T., Szentirmai, É., Kapás, L., & Krueger, J. M. (2011). Energy homeostasis regulatory peptides in hibernating grizzly bears. *General and Comparative Endocrinology*, 172(1), 181-183. <https://doi.org/10.1016/j.ygcen.2010.12.015>
- Garshelis, D., & Steinmetz, R. (2020). *Ursus thibetanus* (amended version of 2016 assessment). The IUCN Red List of Threatened Species 2020: e.T22824A166528664. <https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22824A166528664.en>
- Gerstner, K., Liesegang, A., Hatt, J.-M., Clauss, M., & Galeffi, C. (2016). Seasonal body mass changes and feed intake in spectacled bears (*Tremarctos ornatus*) at Zurich Zoo. *Journal of Zoo and Aquarium Research*, 4(3), 121-126. <https://doi.org/10.19227/jzar.v4i3.181>
- 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>

- Goldsborough, Z. (2017). The effect of visitor density on the behaviour of two Siberian tigers (*Panthera tigris altaica*) housed in a zoo enclosure. *Animal Welfare*, 10(2), 169-83.
- Hansen, R. L., Carr, M. M., Apanavicius, C. J., Jiang, P., Bissell, H. A., Gocinski, B. L., Maury, F., Himmelreich, M., Beard, S., Ouellette, J. R., & Kouba, A. J. (2009). Seasonal shifts in giant panda feeding behavior: Relationships to bamboo plant part consumption. *Zoo Biology*, 29(4), 470-483. <https://doi.org/10.1002/zoo.20280>
- 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>
- Izumiyama, S., & Shiraishi, T. (2004). Seasonal changes in elevation and habitat use of the Asiatic black bear (*Ursus thibetanus*) in the Northern Japan Alps. *Mammal Study*, 29(1), 1-8. <https://doi.org/10.3106/mammalstudy.29.1>
- Jakob-Hoff, R., Kingan, M., Fenemore, C., Schmid, G., Cockrem, J. F., Crackle, A., Bommel, E., Connor, R. & Descovich, K. (2019). Potential impact of construction noise on selected zoo animals. *Animals*, 9(8), 504. <https://doi.org/10.3390/ani9080504>
- Jones, H., McGregor, P. K., Farmer, H. L. A., & Baker, K. R. (2016). The influence of visitor interaction on the behavior of captive crowned lemurs (*Eulemur coronatus*) and implications for welfare. *Zoo Biology*, 35(3), 222-227. <https://doi.org/10.1002/zoo.21291>
- Joshi, A. R., Garshelis, D. L., & Smith, J. L. D. (1997). Seasonal and habitat-related diets of sloth bears in Nepal. *Journal of Mammalogy*, 78(2), 584-597. <https://doi.org/10.2307/1382910>
- Kelly, K. R., Harrison, M. L., Size, D. D., & MacDonald, S. E. (2015). Individual effects of seasonal changes, visitor density, and concurrent bear behavior on stereotypical behaviors in captive polar bears (*Ursus maritimus*). *Journal of Applied Animal Welfare Science*, 18(1), 17-31. <https://doi.org/10.1080/10888705.2014.924832>
- 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>
- Larsen, M. J., Sherwen, S. L., & Rault, J.-L. (2014). Number of nearby visitors and noise level affect vigilance in captive koalas. *Applied Animal Behaviour Science*, 154, 76-82. <https://doi.org/10.1016/j.applanim.2014.02.005>
- Law, G., & Reid, A. (2010). Enriching the lives of bears in zoos. *International Zoo Yearbook*, 44(1), 65-74. <https://doi.org/10.1111/j.1748-1090.2009.00096.x>
- Lenth, R. V. (2020). *emmeans: Estimated marginal means, aka least-squares means*. [Computer software]. R package (version 1.5.3). <https://CRAN.R-project.org/package=emmeans>
- Lesmerises, R., Rebouillat, L., Dussault, C., & St-Laurent, M.-H. (2015). Linking GPS telemetry surveys and scat analyses helps explain variability in black bear foraging strategies. *PLOS ONE*, 10(7), e0129857. <https://doi.org/10.1371/journal.pone.0129857>
- Lewis, R. N., Chang, Y., 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>
- Li, Y., Swaisgood, R. R., Wei, W., Nie, Y., Hu, Y., Yang, X., Gu, X., & Zhang, Z. (2017). Withered on the stem: Is bamboo a seasonally limiting resource for giant pandas? *Environmental Science and Pollution Research*, 24(11), 10537-10546. <https://doi.org/10.1007/s11356-017-8746-6>
- Liu, H., Duan, H., & Wang, C. (2017). Effects of ambient environmental factors on the stereotypic behaviors of giant pandas (*Ailuropoda melanoleuca*). *PLOS ONE*, 12(1), e0170167. <https://doi.org/10.1371/journal.pone.0170167>
- Lüdecke, D., Makowski, D., Waggoner, P., & Patil, I. (2020). performance: an R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6(60), 3139. <https://doi.org/10.21105/joss.03139>.
- Lukas, K. E., Hoff, M. P., & Maple, T. L. (2003). Gorilla behavior in response to systematic alternation between zoo enclosures. *Applied Animal Behaviour Science*, 81(4), 367-386. [https://doi.org/10.1016/S0168-1591\(02\)00237-X](https://doi.org/10.1016/S0168-1591(02)00237-X)
- Mason, G. J. (1991). Stereotypies and suffering. *Behavioural Processes*, 25(2-3), 103-115. [https://doi.org/10.1016/0376-6357\(91\)90013-P](https://doi.org/10.1016/0376-6357(91)90013-P)
- Mason, G., Clubb, R., Latham, N., & Vickery, S. (2007). Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science*, 102(3-4), 163-188. <https://doi.org/10.1016/j.applanim.2006.05.041>

- Mewada, T., & Dharaiya, N. (2010). Seasonal dietary composition of sloth bear (*Melursus ursinus*) in the reserve forest of Vijaynagar, North Gujarat, India. *Regional office for Asia and the Pacific*.
- Mosnier, A., Ouellet, J.-P., & Courtois, R. (2008). Black bear adaptation to low productivity in the boreal forest. *Écoscience*, 15(4), 485–497. <https://doi.org/10.2980/15-4-3100>
- Mowat, G., & Heard, D. C. (2006). Major components of grizzly bear diet across North America. *Canadian Journal of Zoology*, 84(3), 473–489. <https://doi.org/10.1139/z06-016>
- Munro, R. H. M., Nielsen, S. E., Price, M. H., Stenhouse, G. B., & Boyce, M. S. (2006). Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. *Journal of Mammalogy*, 87(6), 1112–1121. <https://doi.org/10.1644/05-MAMM-A-410R3.1>
- Nelson, O. L., & Robbins, C. T. (2010). Cardiac function adaptations in hibernating grizzly bears (*Ursus arctos horribilis*). *Journal of Comparative Physiology B*, 180(3), 465–473. <https://doi.org/10.1007/s00360-009-0421-x>
- Nelson, R. A., Folk, G. E., Pfeiffer, E. W., Craighead, J. J., Jonkel, C. J., & Steiger, D. L. (1983). Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *Bears: Their Biology and Management*, 5, 284. <https://doi.org/10.2307/3872551>
- Nie, Y., Speakman, J. R., Wu, Q., Zhang, C., Hu, Y., Xia, M., Yan, L., Hambly, C., Wang, L., Wei, W., Zhang, J., & Wei, F. (2015). Exceptionally low daily energy expenditure in the bamboo-eating giant panda. *Science*, 349(6244), 171–174. <https://doi.org/10.1126/science.aab2413>
- Owen, M. A., Hall, S., Bryant, L., & Swaisgood, R. R. (2014). The influence of ambient noise on maternal behavior in a Bornean sun bear (*Helarctos malayanus euryspilus*). *Zoo Biology*, 33(1), 49–53. <https://doi.org/10.1002/zoo.21105>
- Owen, M. A., Swaisgood, R. R., Czekala, N. M., Steinman, K., & Lindburg, D. G. (2004). Monitoring stress in captive giant pandas (*Ailuropoda melanoleuca*): Behavioral and hormonal responses to ambient noise. *Zoo Biology*, 23(2), 147–164. <https://doi.org/10.1002/zoo.10124>
- Ozella, L., Anfossi, L., Di Nardo, F., & Pessani, D. (2017). Effect of weather conditions and presence of visitors on adrenocortical activity in captive African penguins (*Spheniscus demersus*). *General and Comparative Endocrinology*, 242, 49–58. <https://doi.org/10.1016/j.ygcen.2015.12.002>
- Pereira, G. H. A. (2019). On quantile residuals in beta regression. *Communications in Statistics - Simulation and Computation*, 48(1), 302–316. <https://doi.org/10.1080/03610918.2017.1381740>
- Perkins, D. R., & Debbage, K. G. (2016). Weather and tourism: Thermal comfort and zoological park visitor attendance. *Atmosphere*, 7(3), 44. <https://doi.org/10.3390/atmos7030044>
- Prajapati, U., & Koli, V. K. (2020). A comparison of sloth bear (*Melursus ursinus*) diurnal activity between winter and summer seasons in captivity. *Proceedings of the Zoological Society*, 73(4), 400–405. <https://doi.org/10.1007/s12595-020-00345-3>
- Quadros, S., Goulart, V. D. L., Passos, L., Vecchi, M. A. M., & 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>
- Rog, J. E., Lukas, K. E., & Wark, J. D. (2015). Social and environmental influences on pacing in a female Malayan sun bear (*Helarctos malayanus*). *Journal of Zoo and Aquarium Research*, 3(4), 151–156. <https://doi.org/10.19227/jzar.v3i4.148>
- Rose, P. E., Scales, J. S., & Brereton, J. E. (2020). Why the “visitor effect” is complicated. Unraveling individual animal, visitor number, and climatic influences on behavior, space use and interactions with keepers—A case study on captive hornbills. *Frontiers in Veterinary Science*, 7, 236. <https://doi.org/10.3389/fvets.2020.00236>
- Ross, S. R. (2006). Issues of choice and control in the behaviour of a pair of captive polar bears (*Ursus maritimus*). *Behavioural Processes*, 73(1), 117–120. <https://doi.org/10.1016/j.beproc.2006.04.003>
- Ross, M. R., Niemann, T., Wark, J. D., Heintz, M. R., Horrigan, A., Cronin, K. A., Shender, M. A., Gillespie, K. (2016). *ZooMonitor* (Version 1) [Mobile application software]. <https://zoomonitor.org>
- Ryan, J. C. (2016). Impact of an enclosure rotation on the activity budgets of two zoo-housed giant pandas (*Ailuropoda melanoleuca*): An observational case study. *Eat, Sleep, Work*, 1(1), 24–33.
- Scotson, L., Fredriksson, G., Augeri, D., Cheah, C., Ngoprasert, D., & Wai-Ming, W. (2017). *Helarctos malayanus* (errata version published in 2018). *The IUCN Red List of Threatened Species 2017*: e.T9760A123798233. <https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T9760A45033547.en>
- Sellinger, R. L., & Ha, J. C. (2005). The effects of visitor density and intensity on the behavior of two captive jaguars (*Panthera onca*). *Journal of Applied Animal Welfare Science*, 8(4), 233–244. [https://doi.org/10.1207/s15327604jaws0804\\_1](https://doi.org/10.1207/s15327604jaws0804_1)



- Schaller, G. B. (1985). *Giant pandas of Wolong*. University of Chicago Press.
- Shanmugam, A. A., Kumar, J. K., Selvaraj, I., & Selvaraj, V. (2011). Effects of body weight and season on serum lipid concentrations in sloth bears (*Melursus ursinus ursinus*). *Journal of Zoo and Wildlife Medicine*, 42(3), 373–381. <https://doi.org/10.1638/2008-0213.1>
- 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., Hemsworth, P. H., Butler, K. L., Fanson, K. V., & Magrath, M. J. L. (2015). Impacts of visitor number on kangaroos housed in free-range exhibits. *Zoo Biology*, 34(4), 287–295. <https://doi.org/10.1002/zoo.21226>
- Sherwen, S. L., Magrath, M. J. L., Butler, K. L., Phillips, C. J. C., & Hemsworth, P. H. (2014). A multi-enclosure study investigating the behavioural response of meerkats to zoo visitors. *Applied Animal Behaviour Science*, 156, 70–77. <https://doi.org/10.1016/j.applanim.2014.04.012>
- Soriano, A. I., Vinyoles Cartanyà, D., Maté García, C. (2013). The influence of visitors on behaviour and on the use of space in two species of ursids: A management question? *International Zoo News*, 60(5), 341-356. <http://hdl.handle.net/2445/98903>
- Spady, T. J., Lindburg, D. G., & Durrant, B. S. (2007). Evolution of reproductive seasonality in bears. *Mammal Review*, 37(1), 21–53. <https://doi.org/10.1111/j.1365-2907.2007.00096.x>
- Stirling, I., & Derocher, A. E. (1990). Factors affecting the evolution and behavioral ecology of the modern bears. *Bears: Their Biology and Management*, 8, 189-204. <https://doi.org/10.2307/3872919>
- 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: Visitor effects on gorilla behaviour. *Zoo Biology*, 31(5), 586–599. <https://doi.org/10.1002/zoo.20425>
- Suárez, P., Recuerda, P., & Arias-de-Reyna, L. (2017). Behaviour and welfare: The visitor effect in captive felids. *Animal Welfare*, 26(1), 25–34. <https://doi.org/10.7120/09627286.26.1.025>
- 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>
- Wagman, J. D., Lukas, K. E., Dennis, P. M., Willis, M. A., Carroscia, J., Gindlesperger, C., & Schook, M. W. (2018). A work-for-food enrichment program increases exploration and decreases stereotypies in four species of bears. *Zoo Biology*, 37(1), 3–15. <https://doi.org/10.1002/zoo.21391>
- Watters, J. V. (2014). Searching for behavioral indicators of welfare in zoos: Uncovering anticipatory behavior. *Zoo Biology*, 33(4), 251-256. <https://doi.org/10.1002/zoo.21144>
- Watts, J. C. (2009). Case study: Seasonal diets for brown bears (*Ursus arctos*) at Brookfield Zoo—successful implementation led to reduced weight and improved behavior. *Proceedings of the Eighth Conference on Zoo and Wildlife Nutrition, AZA Nutrition Advisory Group*, Tulsa, OK.
- Watts, P. D., & Jonkel, C. (1988). Energetic cost of winter dormancy in grizzly bear. *The Journal of Wildlife Management*, 52(4), 654-656. <https://doi.org/10.2307/3800925>
- White, B. C., Houser, L. A., Fuller, J. A., Taylor, S., & Elliott, J. L. (2003). Activity-based exhibition of five mammalian species: Evaluation of behavioral changes. *Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association*, 22(3), 269-285. <https://doi.org/10.1002/zoo.10085>
- Williams, E., Carter, A., Rendle, J., & Ward, S. J. (2021a). Impacts of COVID-19 on animals in zoos: A longitudinal multi-species analysis. *Journal of Zoological and Botanical Gardens*, 2(2), 130–145. <https://doi.org/10.3390/jzbg2020010>
- Williams, E., Carter, A., Rendle, J., & Ward, S. J. (2021b). Understanding impacts of zoo visitors: Quantifying behavioural changes of two popular zoo species during Covid-19 closures. *Applied Animal Behaviour Science*, 236. <https://doi.org/10.1016/j.applanim.2021.105253>
- World Health Organization (2021, October 19). Coronavirus disease (COVID-19) pandemic. <https://www.who.int/emergencies/diseases/novel-coronavirus-2019>
- Yong, Y., Liu, X., Wang, T., Skidmore, A. K., & Prins, H. H. (2004). Giant panda migration and habitat utilization in Foping Nature Reserve, China. In D. Lindburg & K. Baragona (Eds.), *Giant pandas: Biology and conservation* (pp. 159-169). University of California Press. <https://doi.org/10.1525/9780520930162-021>